EUTROPHICATION OF LAKE ELLESMERE: A STUDY OF PHYTOPLANKTON

by

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ABSTRACT

Lake Ellesmere was studied over a two year period from June 1978 to July 1980. Based on whole water samples, the lakewater chemistry was analysed for a range of physical and chemical parameters and these were related to the phytoplankton community dynamics.

The shallow lake (maximum depth 3.02m below m.s.l.) was found to be a very variable environment, due to the exposed nature of the area, the close proximity of the sea and the agricultural catchment. The brackish nature of the lake water was due to seawater influx at times of prolonged openings and the percolation of seawater through the seaward shingle barrier. The lake was very turbid (euphotic depth 0.94m) due to the action of wind maintaining sediment and phytoplankton within the water column. The input of plant nutrients from the catchment showed in the high nitrogen and phosphorus concentrations in the lakewater, with areal loadings for total nitrogen and total phosphorus 10.02 $g.m^{-2}.yr^{-1}$ and 0.287 $g.m^{-2}.yr^{-1}$ respectively. Using a strict definition of trophic state the lake was described as highly eutrophic.

Phytoplankton were counted using a haemocytometer method, and this method was statistically analysed for precision and accuracy. A little-used statistical test, Fisz's k-sample test, was recommended for the routine analysis of counting data. The dominant organisms were green and blue-green species of Dictyosphaerium, Oocystis, Planctonema and Microcystis. One new species was described and tentatively named Lobocystis sp. nov. Many new records of algae were made for New Zealand including Microcystis minutissima, Merismopedia tenuissima, M. punctata, Spirulina major, Oscillatoria subtilissima, Mantoniella squamata, Prymnesium saltans and Pavlova gyrans.

Reciprocal averaging ordination of the phytoplankton population data was undertaken and the first three eigenvalues accounted for 38% of the variability. The ordination axes were correlated with the physico-chemical data, with pH and nitrate nitrogen being most highly correlated. Using nutrient supply ratios, potential nutrient limitation was recognised. Phosphorus was potentially limiting in winter, followed by a brief period of potential carbon limitation in the vicinity of the inflows in spring, and potential nitrogen limitation in summer especially 1980. A shift in the composition of the flora occurred including an increase in blue-green algae during the period of potential nitrogen limitation. The importance of light limitation was also recognised.

CHAPTER 1

INTRODUCTION

Lake Ellesmere is a large shallow lake on the east coast of the South Island and is the fourth largest lake in New Zealand (Figure 1/1). Nearly triangular in shape, it is surrounded on two sides by rich agricultural land from which it receives surface inflows, and on the third side it is bordered by a shingle spit which separates it from the Pacific Ocean.

The lake is a noted wildlife habitat and at one time it supported extensive bird populations, especially black swans, ducks and geese. These wildfowl depended for food and habitat on extensive Ruppia and Potamogeton beds on the shallow margins of the lake. These plant beds were drastically reduced at the end of the 1960's, and have not redeveloped to the same extent since that time. The lake is also an important fishery which is exploited both for commercial and recreational purposes. Other recreational activities on the lake include boating and water skiing.

In the early 1970's, concern developed over the possible deterioration of water quality in the inflow rivers and streams to the lake due to intensification of agriculture and discharge of treated sewage effluent. The possible increase in nutrient content was likely to accelerate eutrophication of the lake, yet there was little scientific basis on which to present this evidence. The concern over the possible deterioration of the lake led to the preparation of a background review study on Lake Ellesmere and its catchment (Hughes et al., 1974).

This present study is a baseline survey of the water quality of Lake Ellesmere. It aims at assessing the trophic status of the lake using chemical and biological parameters and also at identifying the key factors regulating the phytoplankton community within the lake. Using data collected over a two-year period, from June 1978 to July 1980, the study covers the major factors of lake conditions. The physico-chemical features of the inflows, outflow and climate are discussed in Chapter 3; the lake environment in Chapter 4; the

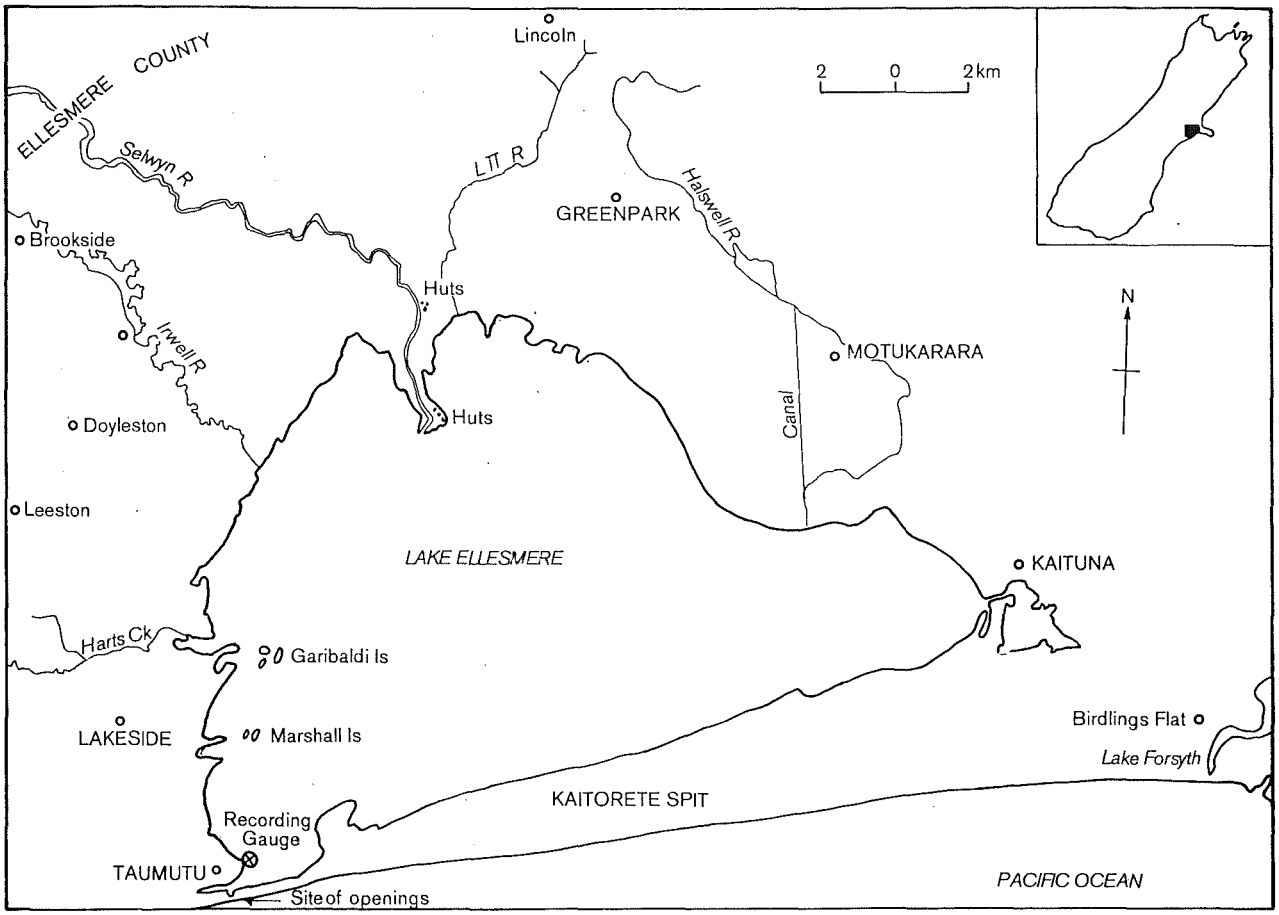


Figure 1/1: Lake Ellesmere and environs.
Source: Hughes, McColl and Rawlence, 1974

phytoplankton flora in Chapter 5 and the phytoplankton community dynamics in Chapter 6. The results from this present study are discussed and compared with other lake systems in Chapter 7.

By way of introduction, some background concepts and data must be introduced so this chapter will examine the theory of eutrophication and the historical background of Lake Ellesmere. These two aspects will be related to the present state of knowledge concerning phytoplankton, especially within New Zealand.

1.1 DEFINITION OF EUTROPHICATION

The development of the concept of eutrophication has been reviewed a number of times (Stewart and Rohlich, 1967; Hutchinson, 1969; Wood, 1975), yet there remain significant variations between authors in the definition of associated terms.

The terms "eutrophic", "mesotrophic" and "oligotrophic" were first employed in a German study by Weber (1907, not seen; cited by Hutchinson, 1969) to describe the general nutrient conditions in the layers formed during the development of peat bogs. In this case nutrient conditions commenced as eutrophic, but progressed towards an oliogtrophic state as a raised bog was built up. The flora characterizing each water type was regarded as a consequence of these trophic conditions.

At about the same time as Weber was writing there was increasing interest in the classification of lakes. A complex terminology began to be developed in recognition of various regional water types. Wesenberg-Lund (1908, not seen; cited by Wood, 1975) and West and West (1909) noted floral differences between lakes of different depths. The deep lakes of Britain and the Swiss Alps had populations of desmids, whereas the shallow lakes of Denmark and Sweden had populations of blue-green algae and diatoms (Wood, 1975). Thienemann (1913, not seen; cited by Hutchinson, 1969) recognised two lake types based on hypolimnetic oxygen concentrations and differences in the benthic chironomid fauna.

The terms oligotrophic and eutrophic were not employed with respect to limnology until 1919, by Naumann (1919, not seen; cited by Hutchinson, 1969). Naumann later defined eutrophication as an increase

of the nutritional standards especially with respect to nitrogen and phosphorus (Naumann, 1931, not seen; cited by Stewart and Rohlich, 1967). He described eutrophic lakes as nutrient rich and oligotrophic lakes as nutrient poor. Unfortunately (through no fault of his) Naumann's chemical analyses were inadequate at the time he developed his classification system, so he distinguished lake types on the basis of the turbidity and discolouration of the water during summer (Hutchinson, 1969).

Hasler (1947) recognized the continuum between the extreme lake types, oligotrophic and eutrophic, and he defined eutrophication as the "enrichment of water be it intentional or unintentional". This definition, like Naumann's, is based on the nutrient content of the water. Hasler used the term mesotrophic to describe the middle range within this continuum.

As the classification of lakes continued, there was confusion between the conditions of production (nutrient supply) and its effects (oxygen depletion, floral composition) (Teiling, 1955; Rodhe, 1969). When these two aspects were coincident all was well, but the trophic terms lost much of their sense as more exceptions were described. Lee (1970) tabulated the general characteristics of oligotrophic and eutrophic lake types using plant production, hypolimnial oxygen content, conductance, biotic numbers as well as plant nutrient fluxes as the distinguishing parameters. Ciecka et al. (1980) also referred to those parameters and added seechi disc depth and chlorophyll'a' concentration as measures of eutrophication.

Many exceptions have been found to the generalized patterns of trophic state (Wood, 1975), and there is real potential for confusion if a strict definition is not adhered to. Stewart and Rohlich (1967) and then Moss (1980) recognized how ambiguous the terminology had become, because of the way in which the concept of eutrophication had developed. Moss preferred to use 'fertile' and 'infertile' when referring to the trophic state of lakes, and insisted that there was a continuum between their extremes. His

view in effect returns to the kind of definition of oligotrophy and eutrophy with which Naumann began the discussion, for it is based on plant nutrient content of the water. This is the definition of eutrophication accepted in this present study.

The role of phytoplankton in eutrophication has been recognised from the earliest classification of lakes by West and West (1909). Applying the strict definition of eutrophication expounded above, phytoplankton parameters can be regarded only as indirect indices of eutrophication. Only measures of nutrient content can provide the trophic status of a water body and the rate of eutrophication.

Formerly, qualitative changes in floral composition were used to indicate the trophic status of a water body. This led to the confusion between the definition of the process of eutrophication and the effects of the process. The change in lake floras was the basis of Nygaard's quotient hypothesis (Nygaard, 1949), in which the relative balance of species of different taxonomic groups indicated the trophic status of a lake. A high proportion of desmids was thought to indicate oligotrophic waters, whereas a dominance of green and blue-green species indicated eutrophy.

Along with qualitative changes in phytoplankton during eutrophication, quantitative changes were also recognised. Rawson (1956) characterized eutrophic lakes as having a large population of a few species, with frequent water-blooms. The most reliable method of measuring phytoplankton biomass (quantity) has been the estimation of cell numbers. Generally, the greater the number of cells the more eutrophic the water will be (Wood, 1975). Because of variations in cell sizes, Findenegg (1974) among others felt that algal numbers alone were not a good index. He suggested that the determination of volumes of algae present in the lake provided a more representative estimate of the standing crop.

Other methods of estimating phytoplankton biomass have included seston concentrations, ash free dry weight and pigment analysis (Wood, 1975).

1.2 LAKE ELLESMERE: HISTORICAL BACKGROUND

From its earliest existence, Lake Ellesmere has been an important visual feature of the landscape of Canterbury. However,

there have been changes in its size and relation to the coast, which are important for any analysis of the present-day lake.

The geological history of Canterbury, including the Ellesmere district, can be determined from Gage (1969) and Fleming (1975). They show that much of the shape of the region was due to the Kaikoura Orogeny in the Pliocene epoch. It was during this time, between 2 and 7 million years ago, that the sea flooded much of Canterbury as far south as Timaru. Towards the end of the epoch the alpine backbone was exposed to erosion and the land grew at the expense of the sea. The volcanoes at Lyttelton were active for the last time during the Pliocene epoch (Fleming, 1975). During the subsequent Pleistocene epoch, there were several oscillations in climate, and resultant fluctuations in the sea-level. Some of the interglacial periods raised the sea-level above the present level, flooding the strait between the gravels of the plains and Banks Island (to use Captain Cook's term, though by then it was inaccurate). At the time of the last glaciation, about 20,000 years B.P., there was a period of outwash and aggradation. The sea-level was much lower than the present level, and as a result the plain was much wider. During the Holocene, the post-glacial age, the uninterrupted warming resulted in a rapid rise in sea-level which lasted from 14,000 to 5,000 years B.P. It was during this latter period that shoreline processes formed the present coastline. With the erosion of sea cliffs and the increase of longshore drift, fed by river estuaries, many shores formed shoals and dunes. This dune development frequently left lakes and swamps behind, and this was how Lake Ellesmere was formed.

Armon (1974) considered that the barrier formed the lake 6000 - 7000 years B.P., and that the spit grew at an angle to the shoreline in the south, across an embayment between the alluvial fan margins and Banks Peninsula. Progradation continued along the full length of the barrier, although retrogradation continued in the south-west. This process still seems to be operating, so that opposite Taumutu the seaward portion of the barrier has now completely gone and only a beach barrier remains.

The vegetation of Canterbury in the pre-colonisation periods has been discussed by Molloy (1969). The general feature of the

landscape was the presence of forest vegetation, including podocarp forests in the lowland regions. The immediate area around the lake was part of the coastal swamp/semi-swamp area which stretched discontinuously from north of Christchurch almost to Timaru. The main species identified from these areas were matai (Podocarpus spicatus), kahikatea (P. dacrydioides), totara (P. totara) and kanuka (Leptospermum ericoides).

Human influence on Lake Ellesmere and its catchment has been comparatively recent. About 950 A.D. moa-hunters occupied the coastal regions of South Island (Johnston, 1969). There were groups of hunters at the south-western end of Banks Peninsula where it meets the plains and at the mouth of the Rakaia River (Straubel, 1957). In a period of about 500 years, the most extensive change to the area occurred with the use of fire (Johnston, 1969). Whether this was deliberate or accidental is uncertain. However the effect was the loss of great areas of forest and the extension of the tussock grasslands (Molloy, 1969). At this time the food of the moa-hunters included birds, seals, shell-fish and other sea-foods, and salt and freshwater fish.

The relationship between the moa-hunters and the Maori is not clear (Johnston, 1969). However the abundance of food in the central region of the South Island led to invasions from the North Island. About four waves of invaders came, including Te Rapuwai, the Waitaha, the Ngati-Mamoe and later the Ngai-tahu (Straubel, 1957). The food for these people from Lake Ellesmere (known as Waihora) included waterfowl, eels, silveries and whitebait. Maori inhabitants were concentrated at the eastern end of the Kaitorete Spit and at Taumutu (Trotter, 1979), and a series of intertribal feuds and rivalries led to a decline in their numbers early in the nineteenth century. The importance of Maori occupancy of the lake area was perhaps more localized but their extraction of timber for building and food from the surrounding swamp and lake waters had long term consequences.

The arrival of the European in Canterbury did not initially affect the Ellesmere district. By the late 1830's whaling stations were being set up on the south side of the Peninsula, and in 1840 Woods and Brown opened a station at Goashore at the eastern end of the Kaitorete spit (Straubel, 1957). This shore station was manned by twenty-four men.

The first attempt at farming the Canterbury Plains was made in 1840 (Straubel, 1957). A group of eight settlers landed at Goashore, and travelling via the Kaitorete Spit and the western side of the lake, made their way to Putaringamotu, beside the Riccarton Bush. This farm was abandoned after about eighteen months due to a dispute over the title of the land. A surveyor for the New Zealand Company, W. Mein Smith (1842; see Straubel, 1957, p.53) described its destruction: "The natives had set fire to the banks of Lake Waihola for the purpose of catching eels, and the fire ran across the plain, destroying the farm in its route."

The Maori route from Banks Peninsula to Otago passed beside the lake, and this was the path which Bishop Selwyn travelled in 1843. On January 9 1843, he left Peraki and walked over the Peninsula to view the lake (Selwyn, 1845). "Within this shingle bank is a great lake, Waihora, filling up the space wrongly marked on the map as a bay of the sea, but really occupied by a freshwater lake, ..." (1845, p.9). The next day they walked along the spit to Taumutu, noting that the "river occasionally breaks into the sea from a heavy flood in the lake." (1845, p.9).

During the years that followed, the land around the lake was slowly surveyed and divided. The Canterbury Association, which was formed in July 1848, sent out Captain Thomas to survey the area with T. Cass and C.O. Torlesse. Torlesse crossed the lake by boat from Taumutu in 1848, and by February 1849 produced a sketch map of the area, subsequently signed by Thomas as Principal Surveyor (frontispiece to Maling (ed.), 1958). This map showed Lake Ellesmere as having a surface area of 74,000 acres extending into the valleys of Banks Peninsula.

The Maori name of the lake had been Waihora up until this time. This name meant "water spread out", although it was sometimes mis-spelt Waihola (Andersen, 1927). With the completion of the survey of the area and Thomas's map, the lake was named Lake Ellesmere. The source of this new name has been attributed to the Earl of Ellesmere, a member of the Canterbury Association (Penney, 1979).

An unexplained coincidence in the choice of the name Ellesmere relates to the eutrophic mere of the same name on the Shropshire-Cheshire Plain in England. A series of small meres in that area undergo

the biological phenomenon known locally as the "breaking of the mere", whereby the waters change overnight "to the colour and turbidity of pea soup" (Sinker, 1962: 108). The organisms responsible for this waterbloom phenomenon are planktonic blue-green algae including Anabaena, Aphanizomenon, and Microcystis (Phillips, 1884; Sinker, 1962; Reynolds, 1979). The use of the name Ellesmere by Torlesse may perhaps be more than a fortuitous choice, and relate to the visual similarities. If this could be established, it would imply that Lake Ellesmere was subject to water blooms at the time of European occupation of the area. No other literature has been found to confirm or contradict the visual attributes of the water at that time.

The earliest pastoral licences in the Ellesmere area were not registered until later in 1852, and the majority were issued in 1853 (Penney, 1979). From this period onwards, the area was extensively divided and settled. However the land immediately around the lake was not initially suitable for farming because of the existence of the large swamp. It was estimated to cover 4046 hectares and was impenetrable and overgrown with flax, raupo and toe-toe (Penney, 1979).

The potential farmland flooded by the lake was the subject of many discussions and reports in the years that followed (Press, 1863,1868a,1868b,1872,1875; Bray, 1875; Hardy-Johnston, 1875). Although the Maoris opened the lake eight times after the colonists arrived, between 1852 and 1867, the first European opening was by Chapman in 1868 (Andersen, 1927). On several occasions in the early settlement days, subsequent to European control, the area of the lake was large, up to 75,000 acres (Bray, 1975). This area was substantially greater than the present-day area of the lake (see section 4.1).

Over the past century of European settlement, there has been little scientific study of the lake biology. Many studies and reports have been concerned with the engineering problems of opening the lake to the sea. The 1950's saw several reports of groundwater (Oborn, 1951; 1953; 1957), the adjacent vegetation (Evans, 1953) and water weed beds in the lake (Mason, 1946; 1951). Much of this work was brought together in the D.S.I.R. publication 'Lake Ellesmere - a review of the lake and its catchment' by Hughes, McColl and Rawlence (1974), which included a checklist of algae, by Flint, as an

appendix. At about the same time, Burnet and Wallace (1973) compared the trout environment of several New Zealand lakes and suggested that of those studied, Ellesmere was one of the most eutrophic.

Since 1974, the scientific work carried out on Lake Ellesmere has been mostly associated with the lake fauna, including the eels (Ryan, 1978; Todd 1981), a parasite in eels (Hine, 1978), trematodes (Jones, 1978), mysids (Waite, 1981) and black swans (Williams, 1979). Dodgshun (1980) has recorded sharks as occasional visitors to the lake, and Taylor (1974) considered the user-conflict between different groups based around the lake. More recently Palmer (1982) prepared a resource investigation report of the Ellesmere area with particular emphasis on the marginal wetlands of the lake and the coastal area.

1.3 PHYTOPLANKTON STUDIES IN NEW ZEALAND

The role of phytoplankton as primary producers within waterbodies is well understood, and yet the present knowledge within the New Zealand context is limited. Cassie summed up the state of knowledge recently as "Up to the present no comprehensive account of the algae from freshwater habitats in New Zealand has been published." (Cassie, 1980:433). This comment preceded a bibliography of relevant and incidental literature, and with subsequent additions (Cassie, 1981) amounted to just over 500 references, including both taxonomic and ecological studies.

From a taxonomic point of view, a compilation of published and unpublished records of species' occurrence in New Zealand is contained in Chapman et al. (1957), Flint (1966) and Sarma and Chapman (1975). These compilations provide a species list and reference to original records, but provide no descriptions of the taxa, synonymy or known distribution. In the light of this lack of comprehensive taxonomic reference for New Zealand species, it has been necessary to draw extensively on Northern hemisphere floras in this study. The only previous algal identification for Lake Ellesmere consisted of a checklist (Flint, in Hughes et al., 1974). For this reason the full descriptions of the identified phytoplankton have been included as part of this study. Haughey (1968, 1969) used a similar approach for species found in an oxidation pond.

Quantitative ecological studies of New Zealand phytoplankton using direct cell counts have been few. One of the earliest studies

dealt with the abundance of ten species of algae into Lake Sarah, a small oligotrophic lake in the high country of Canterbury (Flint, 1938). More recently Cassie (1969) studied the seasonal succession of phytoplankton in eutrophic Lake Rotorua, a lake which is dominated by diatoms, and has green algae as subdominants. Four further lakes from the Taupo volcanic zone, ranging from oligotrophic to eutrophic, were compared by Cassie (1978). Eutrophic Lake Rotoehu was observed in bloom condition with Aphanizomenon flos-aquae, but generally different diatom species predominated in the three eutrophic Rotorua lakes. In Lake Waikaremoana, an oligotrophic lake, both diatoms and desmids were important components of the flora. Jolly (1977) compared the plankton of several North and South Island lakes using a standardized technique of net hauls and counting, and found Melosira and Dinobryon to be important genera. Burns and Mitchell (1974) did a quantitative survey of the seasonal succession and vertical distribution of phytoplankton in Lake Hayes and Lake Johnson, in Otago. These two eutrophic lakes had floras which differed from one year to another. Blooms of Anabaena flos-aquae occurred frequently, whereas a range of diatoms, dinoflagellates and desmids were important components of the flora at other times. Lam (1981) included quantitative analysis of the phytoplankton of the Waikato River where diatoms predominated, except in the lowland lakes, where blue-green algal blooms were common.

A variety of other methods have been undertaken to assess the importance of phytoplankton in various other lakes. Semi-quantitative abundance scales have been used by Flint (1977) on seven lakes in the thermal region of the North Island; by Flint (1979) on three lakes in Westland, and by Cassie and Freeman (1980) on five dune lakes in Northland. Other methods of estimating phytoplankton standing crop have included chlorophyll 'a' concentrations (Gibbs, 1973) and ATP concentrations (Paerl, 1977). Mitchell (1971) used carbon-14 in a productivity study of three small lakes, including Tomahawk Lagoon.

This present study endeavours to contribute further to the knowledge of phytoplankton within New Zealand through an ecological study of one lake system.

CHAPTER 2

METHODS AND METHODOLOGICAL ANALYSIS

There is very little background data available on the phytoplankton of Lake Ellesmere. It is therefore necessary to provide descriptive information on the phytoplankton of the lake. It is also necessary to construct a predictive model of the phytoplankton population in terms of the lake environment. Cassie (1974) and Venrick (1978a) have both pointed to the importance of stating the objectives of aquatic research, and recognizing the type of data being collected.

This chapter therefore analyses and justifies the statistical methods employed in the study. It outlines the sampling strategy and the procedures of the collecting programme, and divides into three major sections:

1. Sampling strategy, in which the objectives of the study and the theoretical aspects of sampling are considered.
2. Sampling procedure, which describes the collection of field samples, the phytoplankton counting, and the culturing of organisms.
3. Methodological analysis, in which the statistical data are subject to mathematical analysis to determine their credibility. This section can be considered as equivalent to a "control" within an experiment.

2.1 SAMPLING STRATEGY

Initially it was necessary to record the phytoplankton species present within Lake Ellesmere. Previously published studies (Flint, in Hughes et al., 1974) provided an initial checklist, but this was found to be incomplete and some taxonomic names in it needed revision. Extensive samples were collected and analysed, and the correct naming of organisms required a wide literature search. Light and electron microscope techniques were used to study both live and preserved samples. In some cases, cultures were initiated from field

material in order to distinguish rare and small organisms. The findings are presented in the taxonomic data of Chapter 5.

Sampling design in aquatic ecosystems has been discussed in several manuals (Weber (ed.), 1973; Vollenweider (ed.), 1974; Sournia (ed.), 1978). In designing a programme, it is important to set an appropriate level of precision to establish the field distribution of the population, and the variability within it (Venrick, 1978a). Because statistical precision is based on the normal distribution, some element of randomization in the selection of samples is necessary.

Venrick (1978a) has discussed several alternative methods and has argued the advantages of stratified random sampling. In this method complete coverage of the population is ensured without sacrificing randomness. However, the selection of strata is difficult without prior knowledge of the population. Other possible methods include simple random sampling, cluster sampling and systematic sampling. The limitations of these are due either to the difficult logistics of random sampling in a large water body, or the unknown underlying frequency distribution resulting in biased sampling. This bias is due to deviation from the normal frequency distribution. As Cassie (1963) showed, field observations are rarely normal, but may be negative binomial, log-normal, double Poisson, or Poisson-log-normal. Ibanez (1976; not seen cited by Venrick, 1978a) stressed that the conditions demanded by traditional sampling methods were rarely achieved in the planktonic environment. Because of the invisible, mobile nature of the population it is not possible to determine if the same population is being sampled repeatedly. The taking of simultaneous samples, at different locations, and the destructive nature of whole water samples increases the problems of a sampling strategy.

It is important to note that the field distribution of organisms discussed above may be different from the distribution of organisms within a mixed sample. Any sample represents the population at that place, at that time. In order to represent the whole population, the sample needs to be quantified in such a manner as to minimise potential errors (Venrick, 1978b). By thoroughly mixing the sample and drawing small aliquots, it is expected the distribution of organisms would follow the Poisson distribution. This distribution

describes the occurrence of random and rare events which occur independently of one another (Conover, 1980). In the present context, the occurrence of organisms within a mixed sample can be tested against the Poisson distribution to establish that the sample has been thoroughly mixed. The field distribution of organisms in time and space may well diverge from this distribution.

2.2 SAMPLING PROCEDURE

2.2.1 Field Collections

A modified form of stratified random sampling was used without prior knowledge of the populations within the lake. A completely random method was considered impossible because of the difficulty of accurately locating the same random points on each successive visit. It was only possible to have fifteen water samples chemically analysed per month and this imposed some limitation on a more extensive programme.

The sampling was intended to ensure coverage of the whole range of the lake environment. Arbitrary strata were established and the sample stations located within these strata. The allocation of stations was as follows: four stations to sample the major inflows into the lake; four stations out in the lake beyond the inflows, to cover the effect on the lake of the inflows; three stations along the agricultural margins of the lake; two along the shingle spit margin; and two in the central lake area (Table 2/1 and Figure 2/2). Because these strata were arbitrarily chosen, no assessment of the area or volume of each stratum was considered worthwhile.

It proved difficult to locate precise sites within the lake by surveying methods, due to inadequate reference points along two of the lake margins. The designated sample sites were therefore marked with 3.5 m hardwood stakes painted orange for ease of relocation. Thereafter the sites were readily relocated on most return visits to the lake. However, the difficulty of anchoring the boat in some weather conditions meant that the sample could not be taken from exactly the same point on each visit.

Collection of samples from the lake was assisted by the North Canterbury Catchment Board's provision of manpower and transport

Table 2/1: Location of Sampling Sites.

Site No.	Location	Map No.*1	Grid Ref.
1	Lake - off Garibaldi Is.	S93	790235
2	Lake - central	S93	863244
3	Halswell River - pup canal	S84	944305
4	Lake - off Halswell R.	S94	948267
5	Lake - along Spit side	S94	933228
6	Lake - off L II R.	S83	847316
7	L II River	S83	838344
8	Lake - off Selwyn R.	S93	837295
9	Selwyn River - near Lower Huts	S83	830310
10	Lake - in embayment	S83	808308
11	Lake	S93	790272
12	Lake - off Lakeside margin	S93	773202
13	Lake - near Taumutu	S93	772182
14	Lake - along Spit side	S93	843209
15	Harts Ck.	S93	742240

*1 New Zealand Map Series 1, Lands and Survey Department. Scale 1:63360.

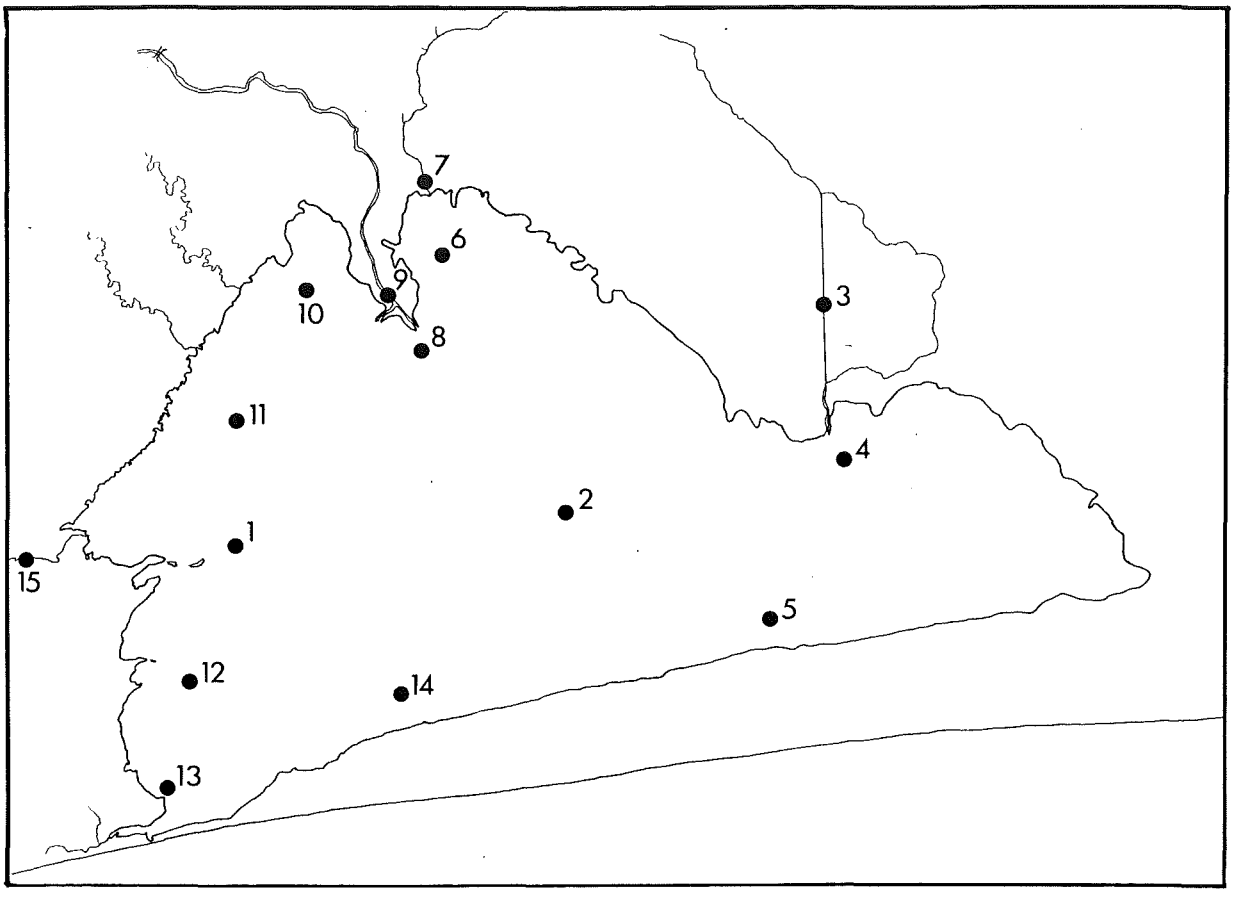


Figure 2/2: Lake Ellesmere: Sampling Sites

facilities, including a 14 foot jet-boat. A separate Catchment Board team gauged the inflows for 19 of the collection dates.

Table 2/3 gives the dates and number of samples collected on each trip to the lake. The trips were made approximately every four weeks over a period of two years, except for a period over spring 1979-1980, when there was fortnightly sampling for selected sites. In total over 342 records for sites were collected, comprising 256 from within the lake and 86 from the four inflows.

The recognised biases in the field sampling were caused by the physical environment. Due to the size of the lake, it was necessary to visit the sites in the same order on each trip, in order to minimise long crossings of the lake, especially head-on into southerly winds. Even so, the sites were always visited between 1000 and 1430 hours.

Furthermore, two whole days were required to complete the laboratory analyses of the changeable nutrients. Consequently trips could only be made on a Monday, Tuesday or Wednesday.

The third, and most important bias in the field sampling was caused by the weather. The lake is exposed and shallow, and therefore subject to wave formation on windy days. In such circumstances, the boat was unstable for instrument readings. Sampling was thus restricted to relatively calm days. As a consequence, the effect of wind on such measurements as sediment suspension was not satisfactorily determined.

On some occasions it was not possible to collect samples at each site. This was due to factors such as low river volume restricting boat access (Site 7), changing weather conditions mid-way through a trip (Collection 12) or low fog making a site impossible to find (Collection 26, site 5).

The sampling for each site included collection of chemical and physical data directly, and the collection of whole water samples for laboratory analyses. The on-board instruments for direct data readings were:

(i) Light meter (Lambda Instrument Corp., Li-Cor model 185A with LI - 192S underwater quantum sensor, calibrated to terrestrial sensor LI - 190S).

Table 2/3: Collection dates and number of samples collected.

Collection number	Date	No. of samples collected		
		Lake	Inflows	Biological analysis*
1	26 June, 1978	11	4	0
2	1 August	11	4	10
3	29 August	11	4	11
4	27 September	11	4	9
5	30 October	11	4	8
6	27 November	11	4	10
7	18 December	11	4	3
8	15 January, 1979	11	4	7
9	26 February	11	4	11
10	26 March	11	4	8
11	1 May	11	4	9
12	28 May	6	1	1
13	3 July	11	4	11
14	28 August	11	4	11
15	12 September	3	0	3
16	26 September	11	4	11
17	10 October	3	0	3
18	7 November	11	3	11
19	27 November	3	0	3
20	11 December	11	3	11
21	22 January, 1980	11	3	8
22	18 February	11	4	8
23	24 March	11	4	10
24	6 May	11	4	10
25	9 June	11	4	9
26	7 July	10	4	10
		256	86	206

* i.e. number of samples counted for phytoplankton standing crop.

(ii) Salinometer (Yellow Springs Instrument Co., Model YSI 33M) for conductivity, salinity and temperature.

(iii) Dissolved oxygen meter (Yellow Springs Instrument Co., Model YSI 57) with salinity compensation, calibrated to atmospheric pressure at the Meteorological Office at Christchurch International Airport (see Table 2/4 for summary, including units of measurement).

Other measurements included estimates of cloud cover, wind direction and on occasions Seechi disc visibility. Supporting climatic data was obtained from the Lincoln College station of the Meteorological Service, the closest available permanent recording station to Lake Ellesmere. This climatic data is summarized for the 14 days preceding each collecting trip and includes the variables listed in Table 2/5.

Whole-water samples were collected with a sampler, with two 2-litre perspex chambers (Fig. 2/6). The sampler was specially designed so that water could move freely through the chamber in the 'open' position. At the desired depth a brass messenger activated the closing mechanism on the sampler. Taps in each chamber allowed the ready transfer of the sample to storage bottles.

The advantages of this sampler were the unrestricted vertical movement of water through the chamber until the sample was taken, and the non-toxic construction material. The use of only perspex, including the lining of the lids, plastic taps and rubber O-rings reduced the possible contamination of samples from the sampler.

Samples for both the biological and chemical analyses were taken from the one sampler collection. From this collection, two separate 1-litre polythylene bottles were filled for chemical analyses of lake samples and three 1-litre bottles for river samples. One bottle from each site was stored immediately on ice for nitrogen and phosphorus analyses. Samples of 300 millilitres were stored in plastic bottles for biological analysis. They were not preserved in the field, but returned in live condition to the laboratory for preliminary observation. Aliquots for counting were always preserved on the same day.

Water samples were delivered to Chemistry Division, Department of Scientific and Industrial Research (D.S.I.R.), Christchurch usually

Table 2/4: Summary of variables measured by field instruments.

Variable	Unit	Method of Measurement
Doxy	ppm	dissolved oxygen. YSI 57
Temp.	°C.	water temperature of sample YSI 33M
Sal.	‰	salinity YSI 33M
Surfli	$\mu E.m^{-2}.s^{-1}$	surface light*1 LiCor 185A 192S
LiOneM	"	light at one metre
LiHalfM	"	light at half metre*2
pH.		triac meter (This meter was found to be unreliable in the field, so pH measures used in analysis based on laboratory measurement by D.S.I.R.)

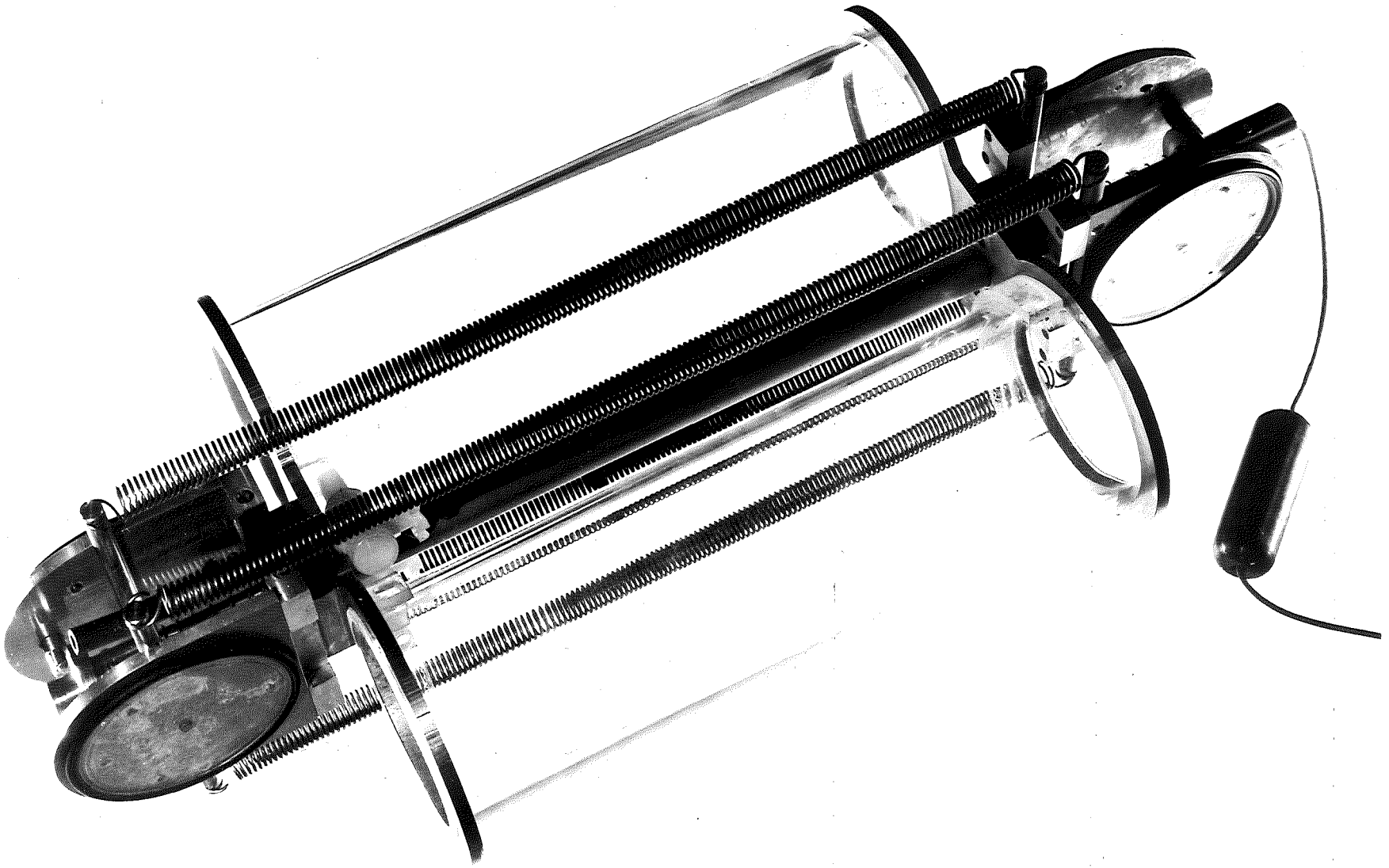
*1 "light" refers to Photosynthetically Active Radiation (PAR), as measured by a quantum sensor.

*2 when the water column was less than one metre the light attenuation was measured at a half-metre depth.

Table 2/5: Summary of climatic variables.

Variable	Units	Description
Cloud	Eighths	Cloud cover in eighths on sample day
Windir		Wind direction in ten degrees at 0900 on sample day
Windfor		Wind force, Beaufort scale, at 0900 hrs on sampling day
Rain	mm	Total rainfall in previous 14 days.
Sunshine	hrs	Mean sunshine hours in previous 14 days
Windrun	Km	Mean daily windrun in kilometres, in previous 14 days

Figure 2/6: Whole-water sampler.



on the day of collection. If this was not possible, they were maintained in cool conditions (5°C) overnight. The methods of analysis of the water chemistry, carried out by D.S.I.R., are summarized in Table 2/7.

2.2.2 Counting Procedure

The advantages of direct counting of samples were discussed by Lund and Talling (1957) and Lund et al. (1958) and include the possible direct observation of cells, the accurate measurement of small populations and the possibility of distinguishing live cells from unwanted debris. With these advantages in mind, the use of a haemocytometer was considered the best available alternative to the recommended inverted microscope method.

A haemocytometer, with improved Neubauer ruling, was loaded with successive drops from a micropipette. The major disadvantage of this counting method was that the depth of the chamber was 0.1 mm, and large organisms could not be evenly distributed within the chamber. Justification for the use of a haemocytometer method in this study was found in the size of the organisms within the flora of Lake Ellesmere. The majority of species were present in units (colonies, unicells or trichomes) of less than 20 µm. Guillard (1978) suggested haemocytometers 0.1 mm in depth were adequate for counting cells with a maximum size of c.30 µm. Thus the distribution within the haemocytometer need not be affected by the depth of the chamber. The use of the haemocytometer allowed for identification of species to provide important data on the population dynamics.

An alternative counting method has been popularized by Utermöhl (1958). It has become known as the "Utermöhl" method, and involves the sedimentation of organisms in chambers (1 - 250 ml) on an inverted microscope. In this way, the organisms are not disturbed in preparation, but are counted directly on the bottom of the counting chamber. This method overcomes the disadvantage of the haemocytometer chamber, because the depth/cell size ratio is much greater. The Utermöhl method has been widely used, including Lund et al. (1958), Uehlinger (1964), Ahlgren (1970), Allen and Koonce (1973), Willén (1976) and Lännergren (1978), and recommended

Table 2/7: Summary of Water Chemistry Analysis Methods used by Chemistry Division, D.S.I.R., Christchurch.

Variable	Units[#2]	Summary of Method [#1]
pH		Radiometer
Conductivity	$mS.m^{-1}$	
Nitrate nitrogen	$g.m^{-3}$	NO_3 quantitatively reduced to NO_2 by cadmium. Difference before and after reduction gives NO_3
Nitrite nitrogen	$g.m^{-3}$	diazontization of sulphanilamide followed by the coupling with naphthylethylene-diamine
Ammoniacal nitrogen	$g.m^{-3}$	indophenal blue reaction
Total organic nitrogen	$g.m^{-3}$	digestion in H_2SO_4 and H_2O_2, followed by ammoniacal determination
Soluble phosphorus	$g.m^{-3}$	acidic ortho-phosphate complexed with molybdate in the presence of antimony, reduced with ascorbic acid
Total phosphorus	$g.m^{-3}$	digestion in H_2SO_4 and H_2O_2, followed by orthophosphate determination
Alkalinity	$g.m^{-3}$	potentiometric titration to different end points: bicarbonate to pH 4.5 carbonate to pH 8.3 free carbon dioxide to pH 8.3
Chloride (as Cl)	$g.m^{-3}$	mercuric nitrate titration
Sulphate (as SO_4)	$g.m^{-3}$	barium perchlorate titration with thoron indicator
Total hardness (as $CaCo_3$)	$g.m^{-3}$	EDTA titration
Calcium	$g.m^{-3}$	EDTA titration
Magnesium	$g.m^{-3}$	EDTA titration
Sodium	$g.m^{-3}$	flame emission spectrometry
Potassium	$g.m^{-3}$	flame emission spectrometry
Reactive silica (as SiO_2)	$g.m^{-3}$	molybdenum yellow reaction
Total suspended solids	$g.m^{-3}$	gravimetric method
Absorbance	-	at 270 nm, 1 cm. after filtration

#1 all analyses on unfiltered whole-water samples.
#2 see Appendix I for comment on SI. units.

by Hobro and Willén (1977). The method has been well described by Margalef (1974) and Hasle (1978a,b).

Venrick (1978b) has reviewed aspects of precision as applied to plankton counting and concluded that there was disparity in recommendations. Lund et al. (1958) have shown that the precision and accuracy of counts by whatever method depends on chosen confidence limits and the total number of organisms counted. Since accuracy is related to the square root of the number of organisms counted, Lund et al. (1958) argued that populations change in abundance within a generation and that therefore an accuracy of ± 50% was often adequate to show such changes. Willén (1976) and Hobro and Willen (1977) recommended an error of estimate approximately ± 20 - 26% of the mean was desirable for routine counting. To achieve this level of accuracy between 60 and 100 individuals needed to be counted. To reduce this error to ± 10%, 400 individuals would need to be counted (Lund et al., 1958).

With particular reference to the use of a haemocytometer, Lund et al. (1958) recommended that a sample be sufficiently rich in organisms to ensure a count of 50 - 100 organisms be made.

Considering the above recommendations, the following method was routinely used. The samples were well shaken on return to the laboratory and 250 ml. was measured into a tall sedimentation chamber (diameter 35 mm. ID). To this was added 5 ml. Lugol's Iodine to give an approximately 2% solution. Lugol's Iodine was recommended because of its preservation of flagellated organisms (Lund et al., 1958; Hobro and Willén, 1977). The samples were allowed to sediment for at least one week before the supernatant was removed, concentrating the sample to 50 ml. The cells were then resuspended by gentle shaking before being split into a 25 ml. stored subsample for reference and a 25 ml. subsample for counting. This sample was therefore 5 times more concentrated than the original lake water. During some collections (trips 2-11) a second stage of concentration reduced the sample volume to 10 ml., thus concentrating the sample to 12.5 times the original lake water. This was discontinued to reduce the possibility of adherence of cells to the sides of the vessels, and also the very concentrated samples tended to be severely clumped in distribution on the haemocytometer. From the concentrated sample, a haemocytometer

was loaded and allowed to sit at least five minutes, giving time for the cells to sink.

The number of preparations was calculated according to the density of the dominant organisms, such that the error level of the estimate was about ± 15-20%. This necessitated counting over 100 units of dispersal (cells, colonies, filaments). Initially only three preparations were counted, but this was increased to six, to reduce the between-preparation variance. When the second stage of sedimentation was discontinued, after Collection 11, the number of preparations was either 10,20 or 30, depending upon the density of organisms.

Despite recommendations to count only the important species (Hobro and Willén, 1977), an attempt was made to record all species present. This posed some problem in identification of the rarest species which were too few for adequate taxonomic examination.

It was not possible to count all the samples collected. This was largely due to over-concentration in early collections; or excessively high sediment content. In total, 206 samples were counted from 25 of the collecting trips (see Table 2/3). Duplicate samples were collected and counted for several early collections. This has allowed a further check on the method of analysis (see section 2.3.3).

2.2.3 Culture Techniques

A variety of culture techniques were used to isolate individual species for taxonomic study. The culture medium used was Bolds Basal medium (Nichols, 1973). However, this was modified to suit the peculiarities of Lake Ellesmere. Since the lake is brackish a range of salinities was used up to 10 ppt.

The basic medium was further modified to bring it closer to the pH range for the lake by replacing K_2HPO_4 with Tris buffer (0.1 M). The Tris buffered medium was adjusted to pH 7.8 - 8.2 before sterilization by either membrane filter (Millipore Corporation 0.45 µm pore size; HAWG 047) or heat. For heat sterilization the medium was modified, following Harrison et al. (1980) by the addition of 1M $NaHCO_3$ and 1N HCl, and autoclaved at 121°C, 15 p.s.i. for 20 minutes. This was left several days before use to allow the equilibrium of the CO_2 system after autoclaving.

Both liquid and solid media were used. The liquid medium was used in crystallising dishes with petri dishes as lids (volume approx. 150 ml), or in stoppered test-tubes. The solid medium was prepared by the addition of bacteriological agar (1.5% W/V), and cultures maintained in standard petri-dishes or on a slope in 25 ml McCartney bottles. The latter preparations were used to maintain stock cultures once an organism had been isolated.

All cultures were grown under fluorescent lighting (40 - 80 $\mu E.m^{-2}.S^{-1}$), at 15-20°C; 12 hours light, 12 hours dark.

2.2.4 Computer Analyses

In this study numerous statistical and computational methods have been used. They were undertaken at the University of Canterbury Computer Centre on Burroughs 6700 and 6900 computers. Four computer packages were used for the majority of the analyses: SPSS, TEDDYBEAR, BIOMASS and H/RECIPAVER.

SPSS: Statistical Package for Social Scientists, version 8. SPSS, 1975; SPSS, 1981). Most of the data was kept on SPSS system files. The subprograms utilised were CONDESCRIPTIVE, NPAR TESTS, NONPAR CORR, PEARSON CORR and FACTOR, as well as other data handling options.

TEDDYBEAR: (1979) was used for nested analysis of variance (section 2.3.3), under the WITHIN option of the package.

BIOMASS: A program to calculate cell volumes based on geometric shape of the cells. This was made available for use in this study by Dr H.C. Duthie (University of Waterloo, Canada), and compiled in Fortran. Each species was approximated to one of six geometric shapes, based on width, length and depth measurements. Table 2/8 gives the six geometric shapes and the computational formulae.

H/RECIPAVER: A program to undertake reciprocal averaging ordination (see Chapter 6). This was made available to Dr A.T. Dobson by Dr N. Mitchell (University of Auckland). Quantitative analysis of cell volume data was used, calculating up to 10 eigenvectors. Output vector loadings for samples were re-entered to SPPS for correlation analysis.

Table 2/8: BIOVOLUME calculations from BIOMASS program.

Shape	Formula		
SP sphere	$\pi/6.1^3$	$0.5236\ 1^3$	
CO cone	$\pi/12.w^2l$	$0.2618\ w^2l$	
DC double cone	$2.\pi/12.w^2.1/2$	$0.2618\ w^2l$	
EL ellipsoid	$\pi/6.w^2l$	$0.5236\ w^2l$	assume w=d
RO rod	$\pi/4.w^2l$	$0.7854\ w^2l$	
TE cuboid	l.w.d.		

2.3 THE METHODOLOGICAL ANALYSIS

In previous sections the strategy of the sampling programme and the method of sampling have been discussed. It now remains to show that the data thus collected fulfilled the expectations of the sampling strategy.

The aspects of the method amenable to statistical analysis were the distribution of organisms on the haemocytometer, the replication of haemocytometer preparations, the analysis of duplicate samples and the calibration of the haemocytometer method against the Utermöhl inverted microscope method.

2.3.1 Distribution of organisms on the haemocytometer

Once water samples were preserved and concentrated, they were mixed to ensure the random distribution of organisms. This distribution, as expressed by the dispersal of organisms on the haemocytometer is therefore expected to follow the Poisson distribution (see section 2.1). Caution is necessary at this point, since Venrick (1978a, p.8) has attributed the Poisson distribution to describe field distributions, using two examples which are clearly related to sampling distributions. The field distribution of organisms is due to temporal or spatial differences within the ecosystem and may be found by comparing the populations of many samples. This field distribution may be quite different from the distribution of a mixed sample, and may involve plankton patchiness or overdispersion. The following discussion relates only to the sampling distribution.

The distribution of cells on a haemocytometer is of historical interest, and it is also relevant in the present situation. In 1907, "Student" described the Poisson distribution based on the distribution of yeast cells in the haemocytometer (Sokal and Rohlf, 1969). The Poisson distribution described the distribution of random and rare events, in which there were many possible loci and the probability of any one locus being occupied was very small, and independent of the occupancy of other loci (Venrick, 1978b). In the present context, the Poisson distribution may be compared with the distribution of phytoplankton to see whether they occur independently and randomly in relation to each other in a thoroughly mixed sample (Sokal and Rohlf, 1969).

The conditions for the variables to fit the Poisson distribution are twofold (Sokal and Rohlf, 1969; Venrick, 1978b). Firstly the criterion of rareness must be fulfilled, and this can be assessed in relation to the maximum possible number of occurrences. Hence in a water sample, the number of cells per millilitre must be small compared with the total possible number of cells which could be contained within 1 millilitre. The second condition for the Poisson distribution is the criterion of independence of occurrence from each other. In this context the distribution of "dispersal units" is what requires testing, not the distribution of cells. Dispersal units may have more than one cell per unit, and consequently the cells are not dispersed independently. To fulfill the criterion of independence "dispersal units" were analysed, and single cells, colonies and filaments were considered of equal value. In reality this may not be true for the size of the unit may influence the overall distribution. This has not been tested in the present context, but in theory the occurrence of a large dispersal unit affects the rarity of the occurrence of a smaller unit (Cassie, 1974). In other words, the space occupied by a large unit reduces the possibility of a smaller unit occupying the same locus.

The counting of the cells on the haemocytometer is the primary level at which data was collected in this study. It is therefore appropriate at this point to test the observed distribution against the expected Poisson distribution, thus giving confidence in calculations based on these data in later sections. Several tests of goodness-of-fit have been described (Sokal and Rohlf, 1969; Norcliffe, 1977; Venrick, 1978b; Steel and Torrie, 1980). The most commonly used is the chi-square (χ^2) goodness-of-fit test (Cassie, 1974). Horn (1977), in reviewing goodness-of-fit tests for discrete data, concluded that this test was often not the most suitable because the distribution of the test statistic only approximated the theoretical chi-square distribution. This approximation was shown to be not very good when the expected class frequencies were small, and it consequently gave a positive bias.

An alternative goodness-of-fit test proposed by Kolmogorov, and extended by Smirnov, overcomes the disadvantages of the chi-square test (Horn, 1977). The Kolmogorov-Smirnov test uses the order of the data, and assumes that the class frequencies are not limited in size. The disadvantage of this test is that it becomes conservative when

parameters are estimated from the data (Norcliffe, 1977), that is, it accepts the null hypothesis when it should be rejected (Type II error). This is overcome, however, with the Lilliefors Test (Conover, 1980).

Because of the widespread use of the chi-square goodness-of-fit test, and the importance of the Kolmogorov-Smirnov test, they will both be discussed and compared with Lilliefors Test on a set of sample data.

2.3.1.1 Chi-square goodness-of-fit test

(Sokal and Rohlf, 1969; Cassie, 1974; Conover, 1980; Steel and Torrie, 1980).

The chi-square (χ^2) goodness-of-fit test assumes the sample is a random sample and the measurement scale is at least nominal. The data are based on observed frequencies (O_j) within grouped classes (j). This is compared with the expected frequencies (E_j) for the same classes. The test statistic is given by

$$T = \sum_{j=1}^{n} \frac{(O_j - E_j)^2}{E_j} \quad \text{(Conover, 1980)}$$

This statistic approximates the chi-square distribution with (n-1-k) degrees of freedom, where k = number of parameters estimated from the sample (Conover, 1980). The null hypothesis, H_o, is that the distribution function of the observed random variable is expressed according to the expected distribution. H_o is rejected if the T statistic exceeds the χ^2 value with the given degrees of freedom, at the $(1-\alpha)$ quantile.

Steel and Torrie (1980) have illustrated the fitting of a Poisson distribution to give the expected frequencies. From the test data, the mean ($\bar{Y}$) is calculated and from this the Poisson distribution can be estimated. The goodness-of-fit test requires the calculation of the T statistic with the (n-2) degrees of freedom, since one parameter is estimated from the data. It has been suggested that pooling of classes takes place when the expected frequencies are less than 1.0 (Steel and Torrie, 1980).

Fitting the Poisson distribution is a laborious process, because the expected frequencies must be calculated from the sample mean, and

as the mean increases, the number of terms to be calculated becomes very large. Tables of the expected values are provided for mean values, but usually only in increments of 0.5 or 1.0 (see Pearson and Hartley (eds.), 1954; Fisz, 1963). However the Poisson was fitted exactly for 18 haemocytometer preparations, and the subsequent chi-square goodness-of-fit test applied. An example is shown in Table 2/9, and the results from all 18 preparations are included in Table 2/10.

It can be concluded from the chi-square goodness-of-fit test that in only one case out of 18 was the null hypothesis rejected at the 95% level. The one preparation rejected was 505D/3 and was not significant at the 99% level.

2.3.1.2 Kolmogorov-Smirnov goodness-of-fit test

(Sokal and Rohlf, 1969; Norcliffe, 1977; Conover, 1980).

The Kolmogorov-Smirnov (K-S) test unlike the chi-square is a non-parametric test which compares the observed distribution with an expected distribution. The test statistic (D) is the maximum absolute vertical distance between these two functions when expressed as relative cumulative frequencies.

The advantage of the K-S test over the chi-square test is that it does not impose limitations on the size of sample and expected frequencies required in classes. The K-S test is exact, even for small samples and assesses the ordinal nature of the data (Norcliffe, 1977; Conover, 1980).

The null hypothesis (H_o) is that the observed distribution, $F(x)$ is equal to the expected distribution, $F^*(x)$, for all values of x. The alternative hypothesis (H_1) is $F(x)$ is not equal to $F^*(x)$ for at least one value of x (the two-tailed test) (Conover, 1980). The null hypothesis is rejected at a chosen level of significance if D exceeds the $(1-\alpha)$ quantile, for the given sample size (n). This test is designed for distributions being specified in advance. When parameters of the test distribution are estimated from the sample, the test becomes more conservative, and the null hypothesis is rejected less often (Norcliffe, 1977).

The K-S test statistic, D, was calculated as the MAX (ABS DIFF) by the NPAR TESTS subprogram, Kolmogorov-Smirnov One-Sample Test (SPSS, 1981). The test statistic was initially calculated for 18

Table 2/9: Chi-squared goodness-of-fit to Poisson distribution.

Sample 502/2.

Y.	Obs.f.	Prob. Equation	Probability	Expected f.	$\frac{(O-E)^2}{E}$
0	1 } 1	$P_0 = e^{-\mu}$	.02423	0.6057 } 2.8594	1.2091
1	0	$P_1 = \mu P_0$	.09015	2.2537	
2	7	$P_2 = \frac{\mu}{2} P_1$	.16767	4.1917	1.8845
3	4	$P_3 = \frac{\mu}{3} P_2$	.20792	5.1980	0.2761
4	5	$P_4 = \frac{\mu}{4} P_3$	.19336	4.8340	0.0057
5	3	$P_5 = \frac{\mu}{5} P_4$	.14386	3.5965	0.0989
6	4	$P_6 = \frac{\mu}{6} P_5$	.08919	2.2297	1.4054
7	0	$P_7 = \frac{\mu}{7} P_6$	.04740	1.1850	
8	1 } 1	$P_8 = \frac{\mu}{8} P_7$	.02204	0.5510 } 2.0905	0.5688
>8	0	$1 - \sum_{i=0}^{8} P_i$	.01418	0.3545	0.5688
$\sum$	25		1.00000	24.9998	5.4485

$\bar{y} = 3.72$

$e^{-\mu} = (e^{-1})^3 (e^{-.72}) = (.36788)^3 (.48675)$

$= .02423$

$n = 7$

$df = 5$

$\chi^2_{(5,95)} = 11.070$

Accept H_o

Table 2/10: Distribution on the Haemocytometer.

Sample		n	χ^2 goodness-of-fit		Kolmogorov-Smirnov and Lilliefors
			T	df(k)	D
502	1	25	5.4838	5	.0791
	2	25	5.4485	6	.0436
	3	25	4.6415	6	.0787
502D	1	25	8.1686	6	.1172
	2	25	8.6632	6	.0833
	3	25	3.9933	7	.1127
504	1	25	2.4018	6	.0644
	2	25	7.0805	6	.0861
	3	25	5.9456	5	.0761
504D	1	25	1.8012	6	.0500
	2	25	10.8219	6	.1213
	3	25	4.2834	6	.0410
505	1	25	4.2278	4	.0753
	2	25	1.1288	5	.0323
	3	25	2.6217	5	.0615
505D	1	25	5.4213	5	.0888
	2	25	6.1491	6	.1168
	3	25	16.3654*	6	.0790
Rejection of H_o			1/18		0/18

Critical values:

χ^2 goodness-of-fit: (Table A_2)*1

p = .95, k = 5, χ^2 = 11.07
k = 6, χ^2 = 12.59
k = 7, χ^2 = 14.07
p = .99, k = 6, χ^2 = 16.81

Kolmogorov-Smirnov: (Table A14)*1

p = .95, n = 25, D = .264

Lilliefors Test: (Table A15)*1

p = .95, n = 35, D = .173

*1 source: Conover (1980)

haemocytometer preparations, the same set used for the chi-square test (section 2.3.1.1). Since the only parameter of the Poisson distribution is the mean, this was calculated from the test data, and the test was anticipated to be conservative. The values for D are presented in Table 2/10, and it may be observed that in no case was the null hypothesis rejected. A further 150 preparations were analysed, and again in no case was the null hypothesis rejected.

2.3.1.3 Lilliefors Test

(Conover, 1980).

The Kolmogorov-Smirnov test has been modified to allow it to be used in situations where parameters were estimated from the data. The test statistic remains the same, but the table of critical values has been recalculated. Lilliefors (1967) presented a table of critical values for the normal distribution. The Poisson distribution, however, approximates the normal distribution for large samples (Steel and Torrie, 1980) and since there are 25 haemocytometer squares in each analysis, the normal approximation is applicable in this context.

Using the Lilliefors critical values a more accurate level of significance can be attained for the K-S D statistic. Even with Lilliefors critical values, it is not possible to reject the null hypothesis for any of the 18 preparations tested (Table 2/10).

In a larger data set of 168 preparations, the distribution of dispersal units within a mixed sample follows the Poisson distribution. In only 4.1% of cases was the hypothesis of the Poisson distribution rejected at the 95% confidence level. Therefore the distribution of dispersal units can be considered to be random within the counting chamber.

This particular analysis has highlighted some deficiencies and limitations of the frequently used goodness-of-fit tests. The recommended analysis for phytoplankton samples is therefore to test with the Lilliefors test statistic. Alternative goodness-of-fit tests are either approximations based on size rather than order, or conservative in nature. Few phytoplankton workers check the basic assumptions associated with the distribution of cells on the counting chamber. This may be due to the use of non-ruled chambers,

so that the data collected is in the form of total organisms per chamber. Most methodological analyses undertaken on phytoplankton data are in terms of the replication of counts, as will be discussed in the next section.

2.3.2 Replication of Haemocytometer Preparations

The problem of replication can best be expressed in terms of the similarity each preparation shows to others taken from the same sample and the extent to which the preparations represent the whole sample. Thorough mixing of the sample before preparations are extracted is the key to equal distribution.

It was shown in the previous section that the distribution of dispersal units on the haemocytometer followed the Poisson and this knowledge will be used in this section. The widely-used test which approximates the chi-square distribution will be compared with tests of the Kolmogorov-Smirnov type.

2.3.2.1 Fisher's Index of Dispersion

Fisher's Index of Dispersion (Fisher, 1948) is found in the literature under various names, including the χ^2 test of randomness (Lund et al., 1958), and the variance test (McAlice, 1971). This test shares the same distribution as the chi-squared goodness-of-fit test, but because it is not identical to it (Cassie, 1974), the alternative name is preferable.

The index of dispersion is a measure of the sample variance against the mean. In the Poisson distribution, this ratio approximates the chi-square distribution with (n-1) degrees of freedom. The test statistic is defined as

$$D = \frac{(n-1)s^2}{\bar{Y}} = \frac{\Sigma(Y-\bar{Y})^2}{\bar{Y}}$$

(Steel and Torrie, 1980). It may be further derived for ease of computation as

$$D = \frac{\Sigma Y^2 - \bar{Y}\Sigma Y}{\bar{Y}}$$

(Lund et al., 1958). Divergence from the randomness essential to the Poisson distribution exists in cases both of overdispersion ($s^2 > \bar{Y}$) and underdispersion ($s^2 < \bar{Y}$). The latter is rare in natural populations (McAlice, 1971).

This index has been put to widespread use in the plankton literature. Lund et al. (1958) and McAlice (1971) used it as a test for randomness on the totals of replicate counts, whereas Hasle (1969) used it on mean counts. Uehlinger (1964) used this index to measure the distribution within the counting chamber, as did both Holmes and Widrig (1956) and Kutkuhn (1958), who used the equivalent ratio ($s^2/\bar{Y}$) measured against the distribution ($\chi^2/(n-1)$). Those who use this index often ignore the limitations associated with it. Rao and Chakravarti (1956) showed that this index depended largely on the magnitude of the Poisson parameter, whereas Frome (1982) also suggested the size of the sample was important.

In the present study 38 samples were subjected to Fisher's Index of Dispersion. The test statistic, D, was calculated following the method outlined by Lund et al. (1958), using the total counts from replicate preparations. The results given in Table 2/11 indicate that out of 38 samples, the null hypothesis that the variance and mean were equal was rejected 10 times. This rate of rejection (26.3%) was high, but with the limitations of this test, consideration is given to other alternative tests.

2.3.2.2 Smirnov k-sample Test

A test of the Kolmogorov-Smirnov type is a possible alternative to the preceding analysis of replicate preparations. The advantage of this test is that it does not assume any underlying distribution and it only tests the maximum absolute difference between two empirical distribution functions. Whereas the Kolmogorov-Smirnov test (section 2.3.1.2) tested a distribution function against a specified distribution, the Smirnov modifications (both 2-sample and k-sample) only test the similarity of the functions (Conover, 1980).

The Smirnov k-sample test assumes that the samples are random, mutually independent of each other, and measured in an ordinal scale (Conover, 1980). The largest observations in each of several preparations are denoted by $Z_1, Z_2, \ldots Z_k$. The sample with the largest Z (i.e. the largest observation over the k replicates) has the empirical

Table 2/11: Replication of Samples

Sample	No. of Reps. k	Fisher's index of dispersion D	Smirnov k-sample		Fisz k-sample	
			Between Reps.	T_3	$\bar{\bar{X}}$	Mn*
503	3	4.25	(1,2)	.20	3.56	.1563
502D	3	4.51	(1,3)	.32	4.05	.1762
504	3	5.51	(1,3)	.16	3.61	.1627
504D	3	1.43	(2,3)	.28	3.65	.1846
505	3	1.34	(1,2,3)	.12	2.60	.0826
505D	3	14.39*	(1,2)	.24	3.98	.2473
602	3	0.41	(1,2)(1,3)	.12	5.38	.2154
602D	3	2.49	(1,2)	.20	5.78	.1946
604	3	8.33*	(2,3)	.44*	6.36	.2697
605	3	1.01	(1,2)	.20	4.97	.1393
606	3	7.27*	(1,3)	.32	3.89	.2146
608	3	2.04	(1,3)	.28	3.62	.2180
610	3	23.86*	(1,3)	.44*	4.34	.3512*
611	3	1.72	(1,3)	.20	5.02	.2358
612	3	0.46	(1,3)(2,3)	.12	5.06	.1757
613	3	2.57	(1,3)	.24	5.25	.1717
614	3	2.48	(1,3)	.32	4.46	.2114
702	3	2.34	(1,2)	.24	4.93	.1946
705	3	5.91	(1,2,3)	.24	4.46	.1879
714	3	7.43*	(1,2)	.44*	5.84	.2457
806	6	3.86	(1,3)(3,5)(3,6)	.28	2.02	.1589
808	6	2.97	(3,6)	.20	1.56	.1779
810	6	2.47	(2,3)	.24	2.26	.1802
811	6	10.79	(4,5)	.32	1.13	.2070
812	6	7.19	(1,5)	.28	1.05	.1963
813	6	5.04	(3,5)	.24	2.33	.2127
814	6	5.80	(3,6)	.24	3.10	.1435
901	6	23.74*	(4,5)	.16	4.00	.3121
902	6	2.24	(1,5)(2,6)(4,5)(4,6)	.24	4.14	.1666
904	6	6.61	(1,3)	.28	3.84	.2601
905	6	20.94*	(2,6)	.60*	5.00	.3050
906	6	13.51*	(2,5)	.28	3.55	.2312
908	6	7.64	(4,6)	.20	5.04	.2865
910	6	17.67*	(4,5)	.52*	4.04	.3003
911	6	23.67*	(4,6)	.56*	3.09	.3573*
912	6	3.29	(3,5)	.16	3.98	.1673
913	6	5.11	(1,5)	.24	3.22	.1165
914	6	4.68	(2,5)	.20	4.40	.2312
Rejection of H_o		10/38		6/38		2/38

Table 2/11 continued on next page.

Table 2/11 Continued.

Critical values:

Fisher's Index of Dispersion: χ^2, k-1 degrees of freedom.

(Table A2 in Conover (1980))

$p = .95, \quad k = 3, \quad \chi^2_2 = 5.99$

$\chi^2_5 = 11.07$

Smirnov k-sample: T_3 (Table A24 in Conover (1980)).

$p = .95, \quad n = 25, \quad T_3 = 9/25$ for $(2 \leqslant k \leqslant 8)$

$= .36$

Fisz k-sample: λ^* (derived, based on Table V111 in Fisz (1963))

$$P(Mn < \lambda) = Q(\lambda)^k$$

at the 95% level

$$P(Mn < \lambda) = Q(\lambda)^k = .95$$

$$= Q(\lambda) = (.95)^{1/k}$$

if k = 3:

$$Q(\lambda) = (.95)^{1/3} = .9830$$

from Table V111, Fisz (1963)

$$\lambda = 1.54$$

but

$$Mn^* = Mn/\sqrt{n} \quad \text{since} \quad D(n,j) = \sqrt{n}\ \sup|S(x) - F(x)|$$

and

$$Mn = \max. D(n,j)$$

therefore

$$\lambda^* = \lambda/\sqrt{n}$$

$$= 1.54/\sqrt{25}$$

$$= .308$$

---

if k = 6:

$$Q(\lambda) = (.95)^{1/6} = .9915$$

$$\lambda = 1.65$$

$$\lambda^* = 1.65/\sqrt{25}$$

$$= .33$$

distribution function denoted by $S^{(k)}(x)$. The sample with the smallest Z is the lowest rank and the distribution function is denoted $S^{(1)}(x)$. The test statistic is defined as the greatest vertical distance between the two functions:

$$T_3 = \sup|S^{(1)}(x) - S^{(k)}(x)|$$

(Conover, 1980). The critical level is chosen for the sample size, n, with k replicates. This test is only appropriate when all samples are of the same size. In this study that is the case. Unfortunately, critical values are only given for $k \leqslant 10$, so that samples of $k > 10$ cannot be accurately tested.

In the present study, the Smirnov k-sample test was applied to the 38 samples analysed previously, using the NPAR TESTS subprogram, Kolmogorov-Smirnov Two-Sample Test (SPSS, 1981). The choice of the replicates to be compared posed some problem, because in many samples there were several replicates sharing the position of smallest Z value or the largest Z value. In these cases, each pair was considered and the one with the maximum T_3 value was chosen. The results for the 38 samples are given in Table 2/11. Of the 38 samples, only 6 samples were rejected by the null hypothesis at the 95% confidence level. This rejection implies that in 15.7% of the samples there were at least two replicates that were not from the same distribution. This test does not specify the distribution, but previous analysis (section 2.3.1) has shown this to be a Poisson distribution.

2.3.2.3 Fisz K-sample Test

A modification of the Smirnov test was suggested by Fisz (1963). He proposed that k samples be drawn from the same specified distribution function, F(x). The Fisz test in this present context is capable of incorporating both aspects previously presented, namely that the replicates are from the same distribution, and that this distribution is the Poisson distribution.

The Fisz test for k samples (Fisz, 1963) assumes that the replicates, $k(k \geqslant 2)$, have the same continuous distribution function F(x), and that in each case a simple sample of size n is drawn. Each observation is an independent random variable, $X_{11}, \ldots, X_{1n}, X_{21}, \ldots,$

X_{2n}, ... , X_{k1}, ... , X_{kn}, with the same distribution divided into k groups. The empirical distribution is denoted $S_{nj}(x)$, for the sample from the jth sample (j = 1,2, ... , k). The test compares the vertical distance between each empirical function, $S_{nj}(x)$, and the given distribution function F(x). The test statistic, M_n is the maximum value, and can be defined

$$D(n,j) = \sqrt{n} \sup |S_{nj}(x) - F(x)|$$

where

$$j = 1,2, \ldots , k.$$

$$M_n = \max_{1 \leqslant j \leqslant k} D(n,j)$$

(Fisz, 1963, p.407). In the present context of the Poisson distribution, F(x) was described as the mean (mean X_n) or $\bar{\bar{X}}$, for this was the best estimate for the Poisson parameter, considering all the available data.

The Fisz k-sample test was applied to the same 38 samples previously discussed using the NPAR TESTS subprogram, Kolmogorov-Smirnov One-Sample test (SPSS, 1981) specifying the POISSON option, and the $\bar{\bar{X}}$ which had been previously calculated. Each replicate (k = 3,6) was tested against the specified function, and the test statistic, M_n*, taken as the maximum value of MAX (ABS DIFF) over the replicates, such that $M_n^* = M_n/\sqrt{n}$ (see footnote to Table 2/11 for explanation).

The test statistic for the 38 samples is included in Table 2/11. Of the 38 samples, only two failed the null hypothesis at the 95% confidence level. It should also be noted that these same two samples (610, 911) also failed the null hypotheses with the Index of Dispersion and Smirnov k-sample Test. The overall rejection rate of 5.2% at the 95% confidence level is very satisfactory compared to the other tests.

The Fisz k-sample test may be regarded as a useful test applicable to the replication of counts within counting chambers. This one test verifies the distribution of the organisms from a specified function and also verifies that the replicates are from the same specified function. It incorporates both aspects presented in sections 2.3.1 and 2.3.2 without the limitations of each individual test:

the laborious fitting of the distribution in the chi-square goodness-of-fit test;

the conservative nature of the Kolmogorov-Smirnov test;

the normal approximation of Lilliefors test;

the problem of ties in the Smirnov test;

or the test of variance with the Index of Dispersion.

Using the results of the above Fisz test as confirmed by the other tests, the sub-sampling error as expressed in the distribution of dispersal units on the haemocytometer, and replication of such preparations from the same sample was about 5.2% at the 95% confidence level.

This analysis of methodology so far presented was based on 38 samples from collections 5 to 9. It comprised 18.4% of the total samples for which phytoplankton counts were made. The recording procedure associated with this analysis was, however, voluminous because each square on each haemocytometer preparation was recorded separately, before summation. In order to reduce this procedure, an abbreviated recording method was adopted so that total counts for each preparation, and in some instances, total counts of multiple replicates were obtained. This prevented complete analysis of samples, but the findings based on nearly 20% of the samples can reasonably be regarded as applicable to all samples because no important change occurred in the methodology. However, the number of organisms counted was always greater than 200, which on occasions resulted from the counting of a greater number of replicates.

2.3.3 Analysis of Duplicate Samples

The enumeration of phytoplankton samples is time consuming and therefore replication at the various levels of the sub-sampling design should be devised to maximize precision. Cost and effort analysis has been used by Uehlinger (1964), McAlice (1971) and Woelkerling et al. (1976) in recommending counting regimes for various counting chambers, and Venrick (1978b) has considered some of the theoretical designs.

Venrick (1978b) suggested the nested analysis of variance (ANOVA) model was appropriate to describe the variance components at each level of the sub-sampling design. This was because of the multi-stage sub-sampling nature of the experimental design, where only a fraction of each sample was analysed at each level. Sokal and Rohlf (1969), Venrick (1978b) and Underwood (1981) discuss aspects of the multi-level nested ANOVA, and Kaatra and Harjula (1976) give an example based on phytoplankton sampling.

The assumptions associated with the use of ANOVA include the requirement for normality of data (Sokal and Rohlf, 1969; Norcliffe, 1977). From previous sections 2.3.1 and 2.3.2, it has been shown that the data followed the Poisson distribution. Consequently an appropriate transformation was $\sqrt{Y+\frac{1}{2}}$ (Sokal and Rohlf, 1969).

In the present study the data used for the analysis of duplicate samples was in part the same as used in sections 2.3.1 and 2.3.2. Duplicate samples were collected at each of four sites (samples 502, 504, 505, 602). From each duplicate sample, 3 haemocytometer preparations were made, with 25 squares counted. The design is shown in Figure 2/12.

The four samples were analysed individually by the WITHIN option of the TEDDYBEAR (1979) package. When transformed, the data fitted closely to the normal distribution as tested by the TEDDYBEAR computer program. TEDDYBEAR used Bartlett's test, skewness, kurtosis and absolute values of residuals to test normality, and in each case the coefficient of variation of the mean was reduced by about one half by the use of the transformation. The coefficient of variation over the four samples analysed ranged from 16.35 to 25.03%. The results of these four analyses are presented as ANOVA tables in Table 2/13.

In only one case (sample 505, among replicates (preparations) tested against within replicates) was a significant result found in the F-test. This means that in the three analyses (502, 504, 602) no significant variance was contributed either by the duplicate samples or by the replicate preparations, and for the sample 505 no significant variance was contributed by the duplication of samples.

Sample 505 requires closer attention. It may be noted from section 2.3.2 that one haemocytometer preparation was significantly different from the others. In Table 2/10, it was shown that the

Table 2/12: Design for Nested ANOVA Model.

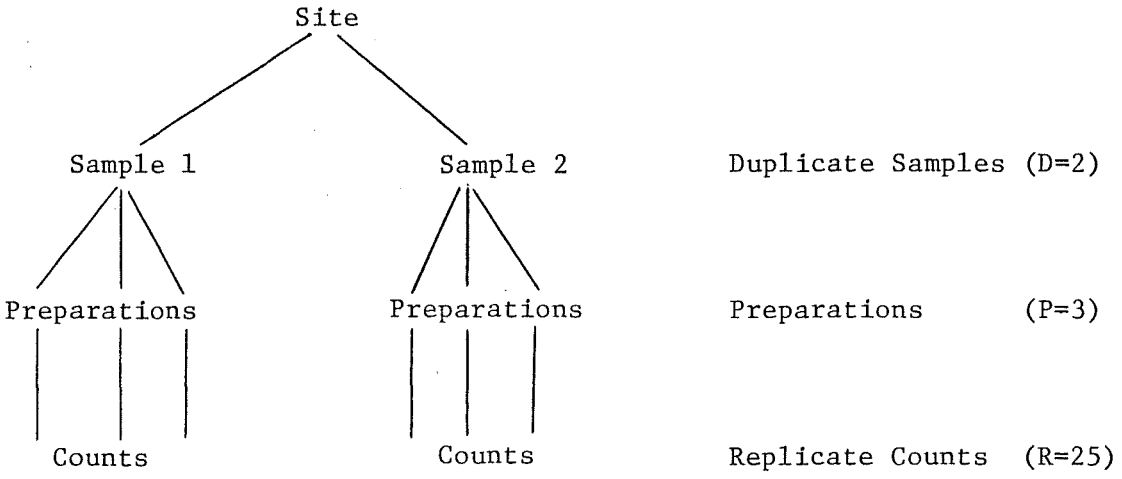


Table 2/13: ANOVA Tables for Duplicate Samples.

Transformation: $\sqrt{Y+\frac{1}{2}}$

Sample 502:

Source of variation	df	MS	F_S
Among duplicates	1	.6133	1.7042 n.s.
Among replicates	4	.3599	1.7958 n.s.
Within replicates (error)	144	.2004	
Total:	149		

Sample 504:

Source of variation	df	MS	F_S
Among duplicates	1	.0050	0.0134 n.s.
Among replicates	4	.2752	1.6562 n.s.
Within replicates (error)	144	.2265	
Total:	149		

Sample 505:

Source of variation	df	MS	F_S
Among duplicates	1	4.9063	6.4824 n.s.
Among replicates	4	.7568	3.4235*
Within replicates (error)	144	.2210	
Total:	149		

Sample 602:

Source of variation	df	MS	F_S
Among duplicates	1	.2980	1.1923 n.s.
Among replicates	4	.2499	1.5781 n.s.
Within replicates (error)	144	.1583	
Total:	149		

Critical values: $p = .95$; $F_{(1,4)} = 7.71$ $F_{(4,144)} = 2.4$

(Conover, 1980, Table A26).

distribution of 505D/3 was significantly different from the Poisson distribution using the chi-square goodness-of-fit test; and in Table 2/11 the replicate samples of 505D were significantly different, using Fisher's index of dispersion. On this basis, sample 505 was re-analysed, using only two replicates for each duplicate sample. The preparations were then known to follow the Poisson distribution, and the transformation of data was appropriate. The revised ANOVA table is presented in Table 2/14. The F-tests in this instance are both non-significant. This indicates that no significant variance was contributed when the assumptions of the analysis were carefully considered.

The variance components at each level can also be calculated following the method of Sokal and Rohlf (1969) for a Model II ANOVA. For comparison these variance components can be expressed as percentages. Table 2/15 gives the percentage variance components for the four samples analysed.

The largest percentage of variance was contributed from within the replicates (preparations). This percentage ranged from 87.83 to 99.56%, and the variance contributed by the other levels, both duplicate samples and replicate preparations, was less than 12%. It may be noted with caution that these levels are low, and that for sample 504, a negative value has been calculated. This is due to the small size of the values in sample 504 as compared with the large component contributed from within the replicates.

This analysis of duplicate samples showed that the greatest variance was contributed from within the preparations, and that the variance among preparations and duplicate samples was very much less. Considering the time and effort involved in counting duplicate samples, the slight amount of additional information was thought unjustified. Consequently, the sampling regime was modified so that duplicate samples were not collected, but the number of replicate preparations counted was increased to reduce the proportion of sample variance.

An interesting extension of this analysis would have been to include the time component of preparing and counting each replicate preparation. This type of analysis has been carried out by Woelkerling et al. (1976) for the Sedgwick-Rafter counting chamber. They were able to make recommendations on their counting regime based on the optimal allocation of the counts for greatest precision in the least time.

Table 2/14: ANOVA Table for 505: Reanalysis.

Transformation: $\sqrt{Y + \frac{1}{2}}$

Sample 505:

Source of variation	df	MS	F_s
Among duplicates	1	1.5456	5.7957 n.s.
Among replicates	2	.2666	1.3153 n.s.
Within replicates	96	.2027	
Total:	99		

Critical values: $p = .95$; $F_{(1,2)} = 18.51$ $F_{(2,96)} = 3.1$

Table 2/15: Percentage Variance Components.

	502	504	505	602
Among duplicates (S^2_A)	1.57	-2.15	11.04	0.3
Among replicates ($S^2_{B \subset A}$)	3.0	2.59	1.08	2.2
Within replicates (S^2)	95.42	99.56	87.83	97.4

2.3.4 Comparison of Counting Methods

At the outset of the present study, an inverted microscope was not available, but towards the end of the sampling period, a Leitz Diavert microscope enabled a comparison of comparable population levels under different counting methods.

Previous comparisons of counting methods have been presented by Uehlinger (1964). In a comparison of the Utermöhl method with the Sedgwick-Rafter chamber under various preparation regimes, Uehlinger was able to present a two-way analysis of variance. He concluded that there was a slight but significant discrepancy between the data obtained using different methods. Because of the nature of the data in the present study, a two-way analysis was not possible.

From the one sample of lake water, multiple sub-samples were taken. One sub-sample was diluted 1:5 and distributed among three 2 ml sedimentation chambers. Within each, from ten fields of view at 400 times magnification, the numbers of seven phytoplankton species were counted (Method A). From another subsample diluted 1:5, three 5 ml sedimentation chambers were prepared, and again from ten fields of view at 630 times magnification, the phytoplankton were counted (Method B). Both of these methods followed the Utermöhl method as described by Hasle (1978a,b). The dense populations allowed for more than 200 organisms to be counted within each chamber, and thus the estimated error was less than 20% (Lund et al., 1958).

Counts were also made of samples using the haemocytometer method (see section 2.2.2). They were obtained by concentration of subsamples by a factor of 5:1, and from each of three replicates, ten preparations were made. The cell counts recorded were totals for each of the seven selected species (Method C). The counts were standardized as a ratio of cells per ml of lake water. Table 2/16 compares the volumes counted and correction factors for each of the three regimes. In this instance, total cell counts were recorded, rather than dispersal units as used in previous sections.

The statistical analysis of the results obtained includes the testing of each replicate sample for the Poisson distribution, using the Fisz k-sample test. Secondly, comparative tests on the different methods were made to test whether the samples were taken from the same population. These tests were both nonparametric

Table 2/16: Comparison of Counting Methods.

	Utermöhl method		Haemocytometer method
	A	B	C
Volume chamber	2 ml	5 ml	0.1 mm^3 = .0001 ml.
Area of chamber (mm^2)	96.42	200.057	1.0
Objective magn.	40	63	25
Diameter field of view (µm)	455	291	n.a.
Area of f. of v. (mm^2)	.1625	.0665	n.a.
Concentration/ dilution factor	1:5	1:5	5:1
Volume lake water counted (ml)*	6.74×10^{-4}	3.32×10^{-4}	5×10^{-4}
Correction factor (cells/ml)*	1483	3008	2000

*Utermöhl method: data recorded per field of view.
Haemocytometer method: data recorded per preparation.

(Mann-Whitney U test, Kruskal-Wallis test) and parametric (t-test).

2.3.4.1 Fisz k-sample Test

Each replicate within each method was tested for randomness using the Poisson distribution by the Fisz k-sample test (Fisz, 1963, see method in section 2.3.2.3). Each replicate included 10 counts, from either haemocytometer preparations or inverted microscope fields of view, with three replicates for each of the three methods. The seven species were counted separately. The test statistic, M_n^*, presented in Table 2/17 is compared with the calculated critical value. In only two of the 21 records was the null hypothesis rejected, i.e. in only two cases was the data not distributed according to the same Poisson distribution within each replicate sub-sample. These two cases were both Dictyosphaerium species, in which the distribution of cells was not random, but concentrated in colonies. Once again the importance of the "dispersal unit" concept can be observed.

This test therefore shows that the data used in this section of the work was largely comparable to that presented in other analyses, and the distribution within the sedimentation chambers followed the Poisson distribution.

2.3.4.2 Mann-Whitney test and Kruskal-Wallis test

These two nonparametric tests are similar, in that the Mann-Whitney test compares two samples and the Kruskal-Wallis test compares k samples, where $k \geqslant 2$ (Conover, 1980). Both tests are based on the comparison of ranked ordinal data. Rank analysis has real advantages, because if the distribution function is not normal, the probability theory is complex, whereas the probability theory based on ranks does not depend on any specified distribution (Conover, 1980).

Both tests assume (Conover, 1980) that the samples are randomly chosen from their respective populations; that each sample is independent; that the populations are mutually independent and that the measurement scale is at least ordinal. The Kruskal-Wallis test also assumes that the k population distribution functions are identical, whereas the Mann-Whitney test assumes that if there is a difference between distribution functions, it is a difference of location of the distribution.

Table 2/17: Fisz test for Poisson distribution

Species Selected	Utermöhl		Haemocytometer
	A	B	C
Pennate diatoms	.3401	.1745	.3020
Tetraedron minimum	.3321	.1935	.2604
Dictyosphaerium pulchellum	.4151	.3775	.6828*
D. ehrenbergianum	.3008	.6203*	.4620
Oocystis parva	.2565	.4694	.2978
O. lacustris	.3745	.3279	.3916
Scenedesmus obliquus	.1384	.2725	.2912

Critical value: λ^* (derived in Table 2/11)

$n = 10,\ k = 3,\ p = .95$

$P(Mn < \lambda) = Q(\lambda)^k$

$Q(\lambda) = .9830$

$\lambda = 1.55$

for $\lambda^* = \lambda/\sqrt{n}$

$= .49$

The null hypotheses state in each case that the test functions are the same as the theoretical functions. The alternative two-tailed hypotheses state that the distribution functions are not identical for at least some values.

Using the data collected under the three regimes, after standardization (see Table 2/16), the Mann-Whitney test was used to compare each of the Utermöhl regimes (A,B) with the haemocytometer regime (C). The Kruskal-Wallis test (k = 3) was used to compare all three methods (A,B,C). Both tests were undertaken with the NPAR TESTS subprogram of the SPSS (1981) package. The respective statistic for each species and each comparison is presented in Table 2/18. The critical value for the Mann-Whitney test was calculated according to Conover (1980, p452 footnote) for n = 30, m = 30, p = .95, and the critical value for the Kruskal-Wallis test was the chi-square approximation for (k - 1) degrees of freedom, corrected for ties.

The results show that when each of the Utermöhl methods was compared with the haemocytometer method, neither comparison failed the null hypothesis for any of the seven species. This shows that under either counting regime, there is no significant difference between the methods when compared on a population basis. When all three regimes are compared using the Kruskal-Wallis test, in 3 out of the 7 species, the null hypothesis was rejected at the 95% level. This implies that at least one of the methods gives larger population levels than one other method, without specifying which method. The three species in which the discrepancy arose were the colonial organisms Dictyosphaerium spp. and Oocystis parva. It has already been shown by the Fisz test (2.3.4.1) that the Dictyosphaerium spp. were not randomly distributed when measured as cells per field of view, and although these non-parametric tests do not rely on the normal distribution function, they do assume randomness with respect to their populations. The colonial nature of these organisms is incompatible with this assumption , and the results obtained are thus unsatisfactory.

2.3.4.3 t-Test

The parametric test comparable to the Mann-Whitney test is the t-test (Conover, 1980). This is a test of the means of two samples, in which the test statistic follows the t-distribution, with (n-2) degrees

Table 2/18: Nonparametric Tests Comparing Methods.

	Mann-Whitney U.		Kruskal-Wallis T (corrected for ties)
	(A-C)	(B-C)	(A-B-C)
Pennate diatoms	429	380	3.721
Tetraedron minimum	419	377	1.623
Dictyosphaerium pulchellum	248	312	9.628*
D. ehrenbergianum	167	239	18.392*
Oocystis parva	135	317	18.991*
O. lacustris	441	358	4.112
Scenedesmus obliquus	409	346	3.374

Critical values:

Mann-Whitney U: Method from footnote to Table A7 (Conover, 1980)

$n = 30, \quad m = 30, \quad x_p = 1.6449, \quad N = n+m$

$$Wp = n(N+1)/2 + x_p\sqrt{nm(N+1)/12}$$

$$= 30(60 + 1)/2 + 1.6449\sqrt{30 \times 30(60 + 1)/12}$$

$$= 1026$$

Kruskal-Wallis T: chi-squared approximation, k - 1 degrees of freedom.

$\chi^2_2 = 5.991$ (Conover, 1980; Table A2).

of freedom. Populations amenable to the t-test must therefore have a normal distribution.

It has been shown previously that the data for this comparison followed the Poisson distribution (2.3.4.1). Therefore a transformation to normality is necessary. Sokal and Rohlf (1969) suggested that the square-root transformation was appropriate for data following the Poisson distribution. For data including zero, the addition of 0.5 before the transformation was required.

The t-test was carried out, after the transformation, using the T-TEST subprogram of the SPSS (1975) package. The first step of this subprogram included the F-test for the homogeneity of variances of the data sets. For cases with unequal variances (rejected H_o of the F-test) an approximation to t was computed, which had the same probability for t with recomputed degrees of freedom (SPSS, 1975; p270). On the outcome of the F-test, the pooled or separated variance estimate for the t-test was chosen. The data sets compared by the t-test were each of the Utermöhl sets (A and B) and the sets combined (A + B) compared with haemocytometer method (C). This gave 3 comparisons, (A v C), (B v C), and (A + B v C), for each of the seven species.

The results for the F-test, and subsequent t-test are shown in Table 2/19. The null hypothesis of homogeneity of variances failed in different numbers of cases for different data sets. The t-test failed the null hypothesis of equality of distribution in 3 out of 7 cases, for each of the three comparisons. The species which were rejected in each test were the same: Dictyosphaerium spp. and Oocystis parva. This therefore was encouragingly consistent with the results obtained from the Kruskal-Wallis test. For the Dictyosphaerium spp. the Poisson distribution was not initially shown, and therefore the square-root transformation could not be validated. These same three sets of data, expressing colonial organisms as cell numbers failed the hypothesis of equality of distribution in both tests.

To conclude, there was no significant difference between the population levels for the non-colonial species. With the Mann-Whitney test, none of the comparisons gave significant differences, whereas the Kruskal-Wallis test showed significant differences for the colonial organisms recorded as cell numbers. The parametric t-test gave very similar results. For the solitary species and the colonial organisms

Table 2/19: Parametric tests comparing methods: F and t-tests.

	A v C		B v C		A + B v C	
	F	|t|	F	|t|	F	|t|
Pennate diatoms	3.01*	1.25	1.50	1.44	1.02	0.34
Tetraedron minimum	1.33	0.33	1.35	1.35	1.33	0.99
Dictyosphaerium pulchellum	3.95*	3.37*	1.70	2.34*	2.38*	3.06*
D. ehrenbergianum	2.27*	4.17*	1.35	3.81*	1.13	4.61*
Oocystis parva	2.13*	5.40*	1.72	2.29*	1.14	4.03*
O. lacustris	1.46	0.02	1.45	1.22	1.08	0.75
Scenedesmus obliquus	3.20*	0.24	1.04	1.52	1.40	0.86

Critical values: p = .95

F test: For (A v C) and (B v C): $k_1 = 30$, $k_2 = 30$, F = 1.84;

For (A+B v C): $k_1 = 30$, $k_2 = 60$, F = 1.65.

(Conover, 1980, Table A26).

t-test: Various degrees of freedom, as calculated by SPSS (1975, p.269).

The t distribution Table A25 (Conover, 1980).

with few cells per colony, there was no significant difference shown between the Utermöhl and haemocytometer methods.

It has thus been shown in the analysis of the method that:

1. the distribution of organisms on the haemocytometer is random;
2. replicate preparations are similar;
3. duplicate samples are similar;
4. the haemocytometer counting method gives similar results to the Utermöhl method, when allowance is made for colonial organisms.

CHAPTER 3

INFLOWS, OUTFLOW AND CLIMATE

Lake Ellesmere is located at the seaward side of the Central Canterbury Plains and its catchment area is largely composed of rich agricultural land. The lake is influenced by the runoff from the agricultural area and also by seawater intrusion, due to the close proximity of the sea.

This chapter discusses the contribution to Lake Ellesmere by the inflows; the nature of the outflow from the lake, and the climate of the area.

3.1 INFLOWS

Five rivers and thirty-two drains are the main discrete inflows into Lake Ellesmere. With the exception of the Selwyn River, they all arise within 19 km of the lake, draining the surrounding agricultural catchment (Hughes et al., 1974). The Selwyn arises in the foothills of the Southern Alps, in the west of the catchment area.

Little published work is available on the inflows. The major rivers have been only infrequently sampled since 1962, and the data are summarised in the review of the lake system by Hughes et al. (1974). The smaller drains are lesser known, except for the Leeston Drain. Marshall (1974) studied the biology of this drain and included chemical analyses taken over a period of several months.

Other inflows into the lake include groundwater percolation, seawater percolation and artesian springs. Little is known about the latter two sources (Speight, 1930; Marshall, 1933; Oborn, 1951).

The groundwater system of the mid-Canterbury region has been subject to careful examination. Whereas previously the origin of the groundwater was thought to be from rainfall (Oborn, 1951), it has now been shown to originate in part from rivers which cross the Canterbury Plain (Wilson, 1973). The permeability of the plain increases eastward, due to gravel sorting and this allows high-yielding aquifers to flow towards the coast. These aquifers are recharged by influent seepage mainly from rivers. Flow patterns have been deduced from piezometric

contours in areas of unconfined water, and can be deduced from pressure differences in confined aquifers. Maps showing the water-table contours are all similar, with nearly parallel contour lines across the plain to the foothills (Wilson, 1973; Hughes et al., 1974; Day and Hunt, 1977; Martin and Noonan, 1977). The water-table is close to the ground surface in the region near the lake, and surface water is therefore drained into Lake Ellesmere.

The influence of rainfall is noticeable in the Ellesmere district. This effect is accentuated at times by increased flow in the rivers which feed water into the unconfined aquifers of the mid-Canterbury plain. Marshall (1933) has also reported "orifices" in the floor of the lake through which water from the raised water-table passes after heavy rainfall.

The land adjacent to Lake Ellesmere is an artesian area which extends north to metropolitan Christchurch. Artesian conditions exist when confined ground water rises to the surface under its own pressure (Oborn, 1951). The depth of the aquifer in this artesian zone is variable. It appears closer to the surface at the south-west corner of the lake than it is north of Lakeside. The Halswell River, which feeds into the north-eastern side of the lake, is spring-fed from this artesian aquifer, as are the Avon and Heathcote rivers which flow through Christchurch (Wilson, 1973). It is unlikely that there are artesian springs within Lake Ellesmere itself (Marshall, 1933).

The following discussion of inflows will concentrate only on the four major sources: the Halswell, LII and Selwyn Rivers, and Hart's Creek. The input from the individual drains is probably minimal when compared with the river inflows. Each physico-chemical variable (as defined in Chapter 2, Tables 2/4, 2/5 and 2/7) is discussed in terms of absolute mean levels, the total range and seasonality over the sampling period. These results are compared with the data collected in 1973-74 (D.S.I.R., pers. comm.), and that presented by Hughes et al. (1974).

3.1.1 Hydrology

The inflows to Lake Ellesmere are variable in size, with the Selwyn contributing more than other sources. Table 3/1 shows the mean flow rate for the four waterways in each of the years (July - June) of this study, and for the 1973-74 period.

Table 3/1: Flow Rates of Inflow Rivers $m^3.s^{-1}$ ± S.E.

	1973-74*	1978-79	1979-80	mean 1978-80
Halswell	1.46	2.57 ±0.342	3.06 ±0.958	2.815 ±0.496
L II	2.27	3.76 ±0.254	3.17 0.285	3.59 ±0.208
Selwyn	2.51	7.39 ±2.078	5.39 ±1.782	5.65 ±1.281
Irwell	0.85	-	-	-
Harts Ck.	1.27	2.82 ±0.058	2.76 ±0.099	2.789 ±0.058
Mean	1.67			3.672 ±0.364

*1973-74: Chemistry Division, DSIR, Christchurch. (pers. comm.)

For each of the rivers, the mean recorded flow was greater than for the comparable period in 1973-74. In the case of the LII, the discharge was at least twice the earlier levels. The total range of flow rates for the 1978-80 period was 1.48 - 22.3 $m^3.s^{-1}$, with an overall mean of 3.67 $m^3.s^{-1}$. This data does not include flood levels which were too high for accurate gauging and therefore is a conservative estimate of inflow rate into the lake.

Hughes et al. (1974) have shown higher flow rates, and calculated a mean inflow rate of 9 $m^3.s^{-1}$. This data was based on Langbein's (1932) report, where the inflow rate of water was calculated from the changes in the lake water-level over a long period of time and thus the higher discharges due to river floods were estimated.

The maximum recorded flow rate in the Selwyn for the 1978-80 period was 22.3 $m^3.s^{-1}$. Greater flood flows were unrecorded in this study but have been reported by Hughes et al. (1974), who gave a maximum flow rate of 476 $m^3.s^{-1}$ for an unspecified inlet. Hughes et al. (1974) recalculated Langbein's (1932) data to suggest a maximum possible inflow for all rivers of 840 $m^3.s^{-1}$. This would occur if all waterways were in maximum flood condition.

Figure 3/3A gives the mean flow rate for all the inflows over time for 1978-80. No discernible pattern is apparent, although flood periods have not been monitored.

The final hydrological input to be considered is the input from rainfall over the lake surface. (The occurrence and frequency of rainfall in the Ellesmere district is discussed as a climatic variable (Section 3.3.1)). An estimation of mean annual rainfall input directly into the lake is obtained from the mean annual rainfall and the area of lake surface. The latter is not easily obtained (section 4.1.1), but Table 3/2 gives the estimated mean annual input from rainfall to the area bounded by the 0.99 m contour line. When shown as mean input per second, direct comparison is possible with the river inflows and is of similar magnitude to the mean inflow rate. On an annual basis, it is a significant input into the lake.

3.1.2 Composition of Inflows

The composition of inflow waters is given in Table 3/4, based on 28 variables. These variables are predominantly chemical, although interactive measures are also included. For ease of discussion, the

Table 3/2: Estimated Input from Rainfall.

Area*1	Mean Rainfall*2	Est. Input
181.75 km^2	689 mm	$1.252 \times 10^8 m^3.yr^{-1}$ $\equiv 3.97\ m^3.s^{-1}$

*1 See Table 4/1.

*2 Source: N.Z. Meteorological Service 1973. Lincoln College mean annual rainfall (1941 - 1970).

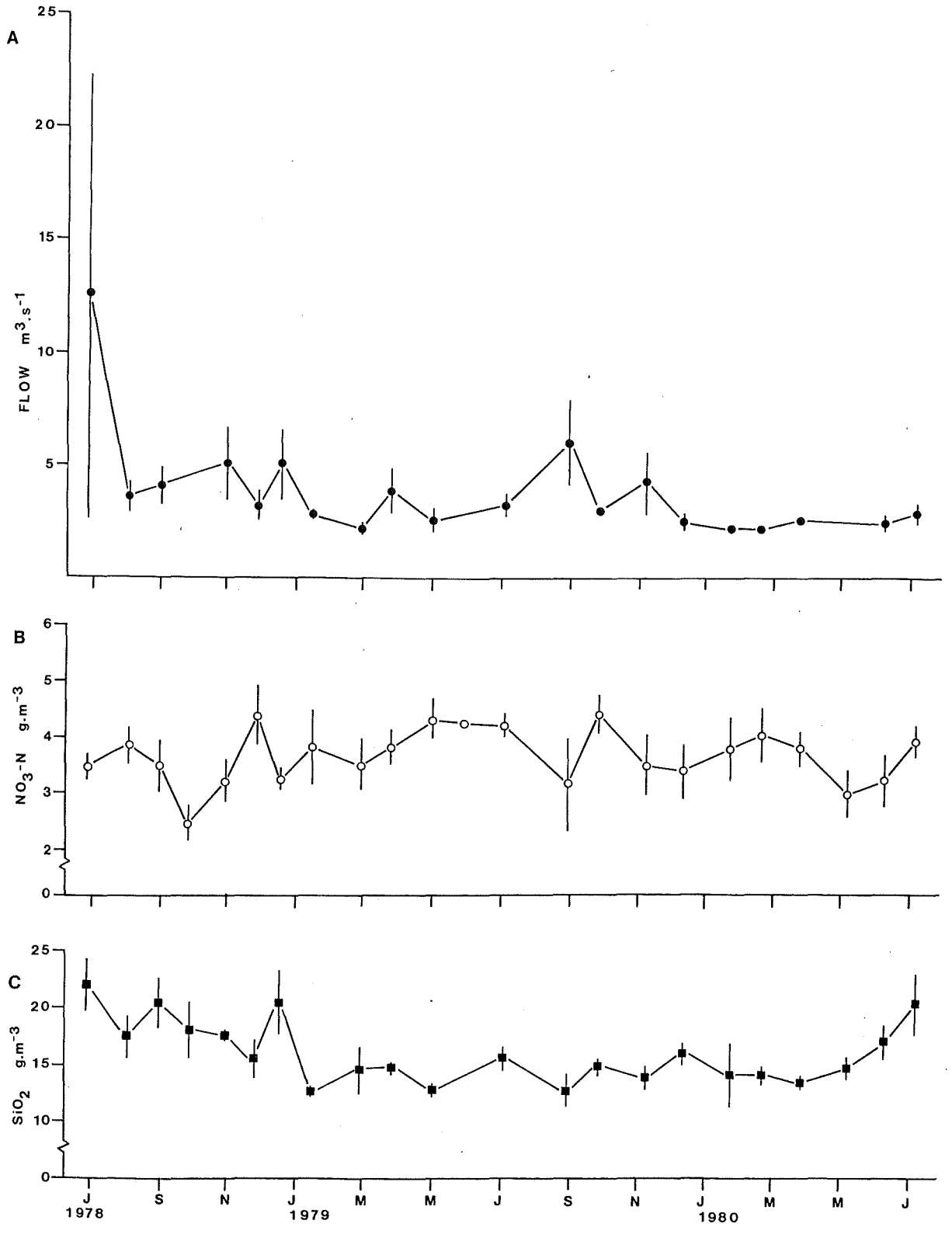


Figure 3/3: A. Mean Flow Rate, 1978-1980 (±S.E.)
B. Mean Nitrate Nitrogen in Inflows (±S.E.)
C. Mean Silica in Inflows (±S.E.)

Table 3/4: Composition of Inflow Rivers (mean ±S.E.)*4

	Units	Halswell R		L II R.	
		1973-4*1	1978-80	1978-4*1	1978-80
pH		7.8	7.435±0.077	7.6	7.260±0.041
conductivity	$mS.m^{-1}$		28.114±0.727		23.225±0.850
total hardness	$g.m^{-3}$	69	91.227±5.390	62	77.350±4.693
Major: Ca^{++}	"	19	23.679±0.786	18	21.192±0.455
Mg^{++}	"	5	6.750±0.366	4	5.385±0.331
Na^{+}	"		25.857±1.402		18.769±0.709
K^{+}	"		3.271±0.447		2.031±0.223
CO_3^{2-}	"		0		0
SO_4^{2-}	"	18	25.929±1.242	14	17.923±0.944
HCO_3^{2-}	"	57	71.565±1.425	58	64.100±0.699
Cl^{-}	"	21	33.500±1.928	17	23.300±1.036
Cases: CO_2	"	4	5.435±0.751	4	6.050±0.587
diss.O_2	"	9	9.108±0.399	8.7	8.490±0.349
Minor: NO_3-N	"	1.6	4.237±0.206	2.0	3.650±0.101
NO_2-N	"	0.024	0.032±0.004	0.014	.017±0.002
NH_4-N	"	0.08	0.098±0.016	0.034	.061±0.013
sol.-P	"	0.042	0.036±0.005	0.026	.027±0.004
tot.-P	"	0.07	0.175±0.041	0.058	.112±0.024
SiO_2	"	16	16.961±0.995	17	16.945±0.710
Organic: T.O.N.	"	0.83	0.656±0.127	0.98	.348±0.087
Trace*3: Fe	"	0.33	0.37	0.25	0.18
Cd	"				<0.01
Cu	"				<0.01
Mn	"				<0.01
Zn	"				<0.01
Sr	"				0.13
Total Suspended Solid	"	169	17.522±6.736	140	6.700±1.532
Absorbance			0.168±0.030		0.073±0.015

Footnotes: *1 1973-74 data Chem. Div. DSIR, (pers. comm.).

*2 1973-74 overall mean includes Irwell River data.

*3 based on one sample, 26 June 1978.

*4 This table appears on one page as Supplementary Table 1.

Table 3/4: Continued.

	Units	Selwyn River		Harts Ck.	
		1973-4*1	1978-80	1973-4*1	1978-80
pH		7.4	7.500±0.084	7.4	7.452±0.030
conductivity	$mS.m^{-1}$		13.779±0.907		19.319±1.224
total hardness	$g.m^{-3}$	49	55.9±8.386	52	57.381±1.131
Major: Ca^{++}	"	12	10.462±0.699	14	16.385±0.428
Mg^{++}	"	5	4.385±0.432	3.6	4.731±0.269
Na^{+}	"		11.154±1.114		13.923±0.512
K^{+}	"		1.392±0.111		1.308±0.091
CO_3^{2-}	"		.318±0.318		0
SO_4^{2-}	"	10	8.154±0.553	12	10.846±0.373
HCO_3^{2-}	"	40	42.955±2.592	48	51.095±0.740
Cl^{-}	"	14	27.667±14.976	14	17.857±0.711
Cases: CO_2	"	2.4	2.636±0.352	3	3.048±0.253
diss.O_2	"	10	10.017±0.387	9	-
Minor: NO_3-N	"	2.2	2.765±0.139	1.6	3.933±0.113
NO_2-N	"	0.006	.006±0.001	0.006	0.004±<0.001
NH_4-N	"	0.015	.036±0.009	0.008	0.028±0.008
sol.-P	"	0.015	.014±0.004	0.026	0.018±0.003
tot.-P	"	0.06	.096±0.023	0.06	0.077±0.021
SiO_2	"	15	12.782±0.362	17	17.662±0.729
Organic: T.O.N.	"	1.2	.250±0.039	0.9	0.191±0.061
Trace*3: Fe	"	0.23	<0.13	0.16	0.10
Cd	"		<0.01		
Cu	"		<0.01		
Mn	"		<0.01		
Zn	"		<0.01		
Sr	"		0.06		
Total Suspended Solid	"	114	20.727±7.05	125	8.467±1.174
Absorbance			0.058±0.007		0.036±0.004

Table 3/4: Continued.

	Units	Mean Inflows 1973-4*2	Mean Inflows 1978-80	Range 1978-80	No samples
pH		7.6	7.415±0.033	6.9-8.9	86
conductivity	$mS.m^{-1}$		21.465±0.742	7.7-39.2	81
total hardness	$g.m^{-3}$	57	71.136±3.087	23-200	81
Major: Ca^{++}	"	11	18.038±0.763	6.5-27	53
Mg^{++}	"	4.5	5.34±0.214	1-9	53
Na^{+}	"		17.585±0.925	7-35	53
K^{+}	"		2.025±0.171	0.4-6.1	53
CO_3^{2-}	"		0.081±0.081	nil-7	86
SO_4^{2-}	"	14	15.906±1.054	4-35	53
HCO_3^{2-}	"	50	57.512±1.455	29-87	86
Cl^{-}	"	17	25.630±3.374	1-280	81
Cases: CO_2	"	3	4.279±0.306	nil-13	86
diss.O_2	"	9.5	9.243±0.240	6.1-12.8	35
Minor: NO_3-N	"	1.85	3.650±0.095	1.5-5.8	86
NO_2-N	"	0.012	0.015±0.002	<0.001-0.089	86
NH_4-N	"	0.031	0.057±0.007	<0.001-0.247	85
sol.-P	"	0.029	0.024±0.002	0.003-0.098	84
tot.-P	"	0.06	0.115±0.015	0.01-0.77	78
SiO_2	"	15	16.059±0.422	8.6-28	86
Organic: T.O.N.	"	0.95	0.375±0.047	0.020-1.99	86
Trace*3: Fe	"	0.18	0.195±0.560		4
Cd	"		<0.01		2
Cu	"		<0.01		2
Mn	"		<0.01		2
Zn	"		<0.01		2
Sr	"		0.095±0.427		2
Total Suspended Solid	"	136	13.616±2.625	<1-134	86
Absorbance			0.086±0.011	0.009-0.476	82

compounds dissolved in the water are divided into five categories, as outlined by Golterman (1975a): major, minor and trace elements, gases and organic compounds. Other compounds, such as silt and clay are suspended within the water column, and may contribute to the chemistry during analysis, whereas the measures of absorbance, pH, conductivity and total hardness express complex interactions within the water chemistry.

3.1.2.1 Major Ions

The samples included in this analysis were collected at sites closer to the lake than those in the 1973-74 survey. The importance of this will be more apparent when consideration is given to the records of chloride, total hardness and conductivity. On occasions, when lake level is high, the lake has some effect on the lower reaches of the Halswell and Selwyn Rivers particularly. In order to give an accurate representation of the inflows, five records of unusually high chloride and conductivity have been deleted from the present analysis.

The major ionic species of the inflows are Ca^{+}, HCO_3^{-}, Na^{+} and Cl^{-}. As would be expected, the Ca^{+} and HCO_3^{-} provide the buffering system and this was reflected in the pH range (section 3.1.2.6.1). The contribution to ionic composition by Na^{+} and Cl^{-} was in part due to the brackish nature of the lake and backflow up the rivers to the point of sampling.

The Halswell had a higher mean concentration of all ionic species than did any of the other three major inflows. The LII had a similar mean calcium level as the Halswell, but otherwise was in the mid-range for most of the ions, as was Hart's Creek. The Selwyn River had the lowest concentrations for several ionic species, except for chloride.

Total hardness is the sum total of divalent cation concentrations. It is assumed in the present study to represent only the calcium and magnesium ions, and is expressed as calcium equivalents. It provides a standardized estimate of divalent cation composition of the water body.

The means and ranges for the inflows for total hardness are given in Table 3/4. The overall mean was 71.136 $g.m^{-3}$, with a range

up to 200 $g.m^{-3}$. The individual inflows show the same pattern of concentrations as the dominant ion calcium.

Some caution must be exercised in comparing the ionic composition of the inflows with the 1973-74 data, since the samples from the Halswell, Selwyn and LII were all collected closer to the lake than previously. Backflow from the lake on occasions affected them. Only Hart's Creek was sampled in the same place, and at a distance great enough to overcome lake influence. Backflow influence was particularly noticeable because of the brackish nature of the lake water. Comparison with 1973-74 data for Hart's Creek showed that there were slight increases in the major ions and total hardness, except for sulphate. The increases were not of sufficient magnitude to constitute an important trend or change in composition.

3.1.2.2 Minor Elements

The distinction between major and minor elements is primarily one of quantity. However there is also biological significance, especially in the case of lakewater (Golterman, 1975a) (see section 4.2). The concentrations of major elements are decisive for the occurrence of many species, while the minor elements will limit the relative and absolute numbers of these organisms. The minor elements are therefore referred to as plant nutrients. In this study the minor elements considered were nitrogen, phosphorus and silica.

3.1.2.2.1 Nitrogen

Nitrogen is found in three inorganic forms: nitrate, nitrite and ammoniacal nitrogen. The latter two are at such low levels that nitrate is the main source of inorganic nitrogen for Lake Ellesmere. The mean values and ranges for these nutrients are given in Table 3/4. The range for nitrate, over 86 samples, was between 1.5 and 5.8 $g.m^{-3}$, with a mean of 3.65 $g.m^{-3}$. The individual inflows showed differences within this range. The Halswell River and Hart's Creek had mean concentrations near 4 $g.m^{-3}$. The differences in these inflow concentrations reflect the source of the rivers. Hart's Creek and the Halswell are slower flowing (section 3.1.1) and pass through intense agricultural areas. The Selwyn has a greater flow and arises further away. The sources of nitrate within the inflows is an important consideration in the

control of supply of the nutrient. The source of the Halswell River is unconfined ground-water which originates in the vicinity of the Waimakariri River (N.C.C.B., pers. comm.). As the ground-water is infiltrated with nutrients and wastes resulting from land use, the nitrate levels rise towards the Lincoln/Halswell area. In a survey (1977-78) of ground-water, levels of up to 10 $g.m^{-3}$ nitrate nitrogen were found (N.C.C.B., pers. comm.).

Nitrite nitrogen has much lower concentrations in all four inflows. The mean concentration over all four was 0.015 $g.m^{-3}$ and the difference between each inflow was also less pronounced. Once again the Halswell had the highest mean concentration, while the LII had about one half the Halswell mean concentration. Both the Selwyn and Hart's Creek were at very low levels.

Ammoniacal nitrogen contributes to the total inorganic nitrogen supply to the lake. The mean concentration over all the monitored inflows was 0.057 $g.m^{-3}$ with a range up to 0.247 $g.m^{-3}$. The individual inflows show a similar pattern to nitrite nitrogen. The Halswell had the highest concentrations, the LII about 60% of that concentration, and both the Selwyn and Hart's Creek had a lower concentration.

Compared with the mean values of the 1973-74 survey, the present figures showed an increase in inorganic nitrogen supply to the lake. This increase was in the form of nitrate nitrogen and ammoniacal nitrogen. Nitrite nitrogen had increased in some of the inflows, but to a very small extent, and barely beyond the range of the standard error of the mean. The nitrate nitrogen showed an overall increase of 1.97 times the mean value, whereas the ammoniacal nitrogen had an increase of 1.83 times. The most noticeable individual changes were nitrate in the Halswell, which had increased 2.62 times, and ammoniacal nitrogen in Hart's Creek, which showed an increase of 3.50 times.

Figure 3/3B shows the mean nitrate nitrogen levels of the inflows over the two-year sampling period. There does not appear to be any seasonal pattern, although there are fluctuations. The lowest mean levels were in spring 1978 with other low concentrations in winter 1979 and autumn 1980. The standard error, as shown graphically, emphasizes the differences between the individual inflows.

The supply of nitrogen to the lake can be better understood when expressed in terms of the quantity flowing over time. Table 3/5 gives the mass-flow for the various inorganic and organic nitrogen forms, and for total nitrogen, in each river and as a total input into the lake. The total nitrogen input to the lake is 57.761 $g.s^{-1}$, approximately 91% as inorganic nitrogen and 9% as organic nitrogen. The inorganic nitrogen is comprised almost entirely of nitrate nitrogen.

It is noticeable that the shortest rivers have the lowest mass-flow, and the lowest standard error. This is probably related to the nature and uniformity of supply from the catchment. In times of little rainfall and low flow, the nitrate concentration builds to high levels within the rivers. When the flow increases after rainfall, the same nitrate supply is diluted within the system. The Selwyn River exhibits a higher standard error as a reflection of its length and varied catchment.

The contribution of inflow inorganic nitrogen to the lake area will be discussed as a "loading" in section 4.2.7.

3.1.2.2.2 Phosphorus

Phosphorus in the inflows is measured in two forms: soluble phosphorus and total phosphorus. There is some doubt as to the forms of phosphorus included within the soluble fraction, although all are considered available for biological use (Chemistry Division, D.S.I.R., pers. comm.). As with inorganic nitrogen, the concentrations of phosphorus within the inflows reflect the origin and passage of the waters through the catchment.

The mean concentration of soluble phosphorus in the inflows was 0.024 $g.m^{-3}$, with a range up to 0.098 $g.m^{-3}$ (Table 3/4). The total phosphorus levels were much greater, with a mean value of 0.115 $g.m^{-3}$, and ranging up to 0.77 $g.m^{-3}$. The Halswell River had the highest concentrations of both soluble and total phosphorus; the LII has the next highest levels; and the Selwyn and Hart's Creek had comparatively less.

Compared with the 1973-74 data (Table 3/4), there was a marked increase in total phosphorus, and a slight decrease in the mean for soluble phosphorus. The total phosphorus level was nearly double, and was apparent in each of the inflows. The decrease in soluble phosphorus was comparatively less (0.82 times).

Table 3/5: Mass-Flow of Nitrogen and Phosphorus ($g.s^{-1}$)

	Halswell	L II	Selwyn	Harts	Total
NO_3-N	11.927	13.104	15.620	10.969	51.620
NO_2-N	0.090	0.061	0.034	0.011	0.196
NH_4-N	0.276	0.219	0.203	0.078	0.776
TOT-INORG-N	12.293	13.384	15.857	11.058	52.592
T.O.N.	1.846	1.379	1.412	0.532	5.169
TOT-N	14.139	14.763	17.269	11.590	57.761
	±13%	±9%	±21%	±5%	
SOL-P	0.101	0.097	0.079	0.050	0.327
	±35%	±23%	±27%	±17%	
TOT-P	0.493	0.402	0.542	0.215	1.652
	±100%	±34%	±17%	±31%	

When total phosphorus is plotted for the two-year period (Figure 3/6A) wide fluctuations are seen. The most noticeable peaks occurred during summer 1978-79, and in the winter of 1979. No single factor can be found to account for this. It is possible that fertiliser application over winter periods gives a winter increase when rainfall leaches the phosphorus into the waterways. The rises in late winter 1978 and winter 1980 tend to confirm this suggestion. The peak in summer, however, cannot be so explained, for analysis of rainfall data (section 3.3.1) gives no supporting evidence. The winter peak of 1979 was due to a high level (0.77 $g.m^{-3}$) in one inflow, the Halswell River. The standard error was very large for this collection date, reflecting the uneven concentrations within the waterways.

A seasonal pattern associated with soluble phosphorus in the inflows is not initially apparent (Figure 3/6B). The peak periods for soluble phosphorus were in early spring 1978 and summer 1980, which did not coincide with the total phosphorus peaks. However, when total rainfall for the 28 days prior to each collection is plotted (Figure 3/6C), it is evident that some relationship exists. The coincidence of the peaks and troughs indicates that soluble phosphorus in the inflows is possibly due to a delayed response to rainfall. It must be noted that the climatic variable ("RAIN") used in computer analyses was defined as the rainfall over the 14 days prior to sampling (Chapter 2, Table 2/5). This did not show the same pattern.

It can be suggested from this analysis that there is a delay period of between 14 and 28 days between the fall of rain and the peaking of soluble phosphorus in the inflow rivers. Unlike nitrate, the soluble phosphorus response to rain and flow is direct. In times of low rain, there are low soluble phosphorus levels, whereas in times of high rainfall and high flow the soluble phosphorus levels also rise. Release from the total phosphorus fraction seems a less likely cause because if that were so a response of total phosphorus to rainfall would be more apparent.

An analysis of phosphorus mass-flow data also diverges from that of nitrate (Table 3/5). The total phosphorus mass-flow into the lake is 1.65 $g.s^{-1}$, of which 0.32 $g.s^{-1}$ is soluble phosphorus. The

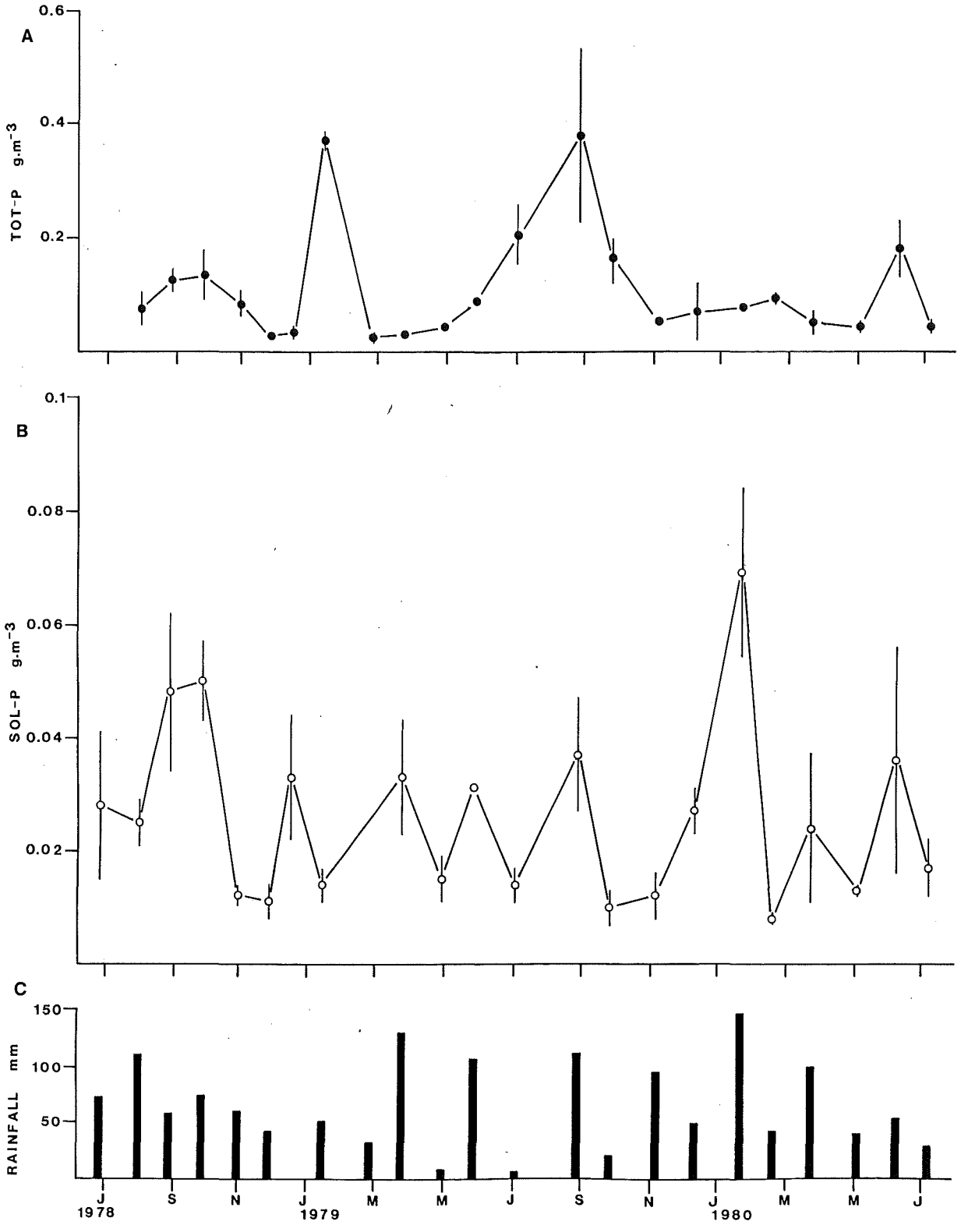


Figure 3/6: A. Mean Total Phosphorus in Inflows (±S.E.)
B. Mean Soluble Phosphorus in Inflows (±S.E.)
C. Rainfall for 28 days prior to sampling

individual inflows show a wide variation in mass-flow. Those from the north-eastern side of the lake, the Halswell and LII, were much greater than the Selwyn and Hart's Creek. The associated standard errors would also show a greater irregularity of mass-flow when compared with the errors associated with nitrate. These differences may probably be interpreted in terms of agricultural practice of the various catchments but further analysis of fertiliser application rates would be required to confirm this aspect. Certainly the phosphorus supply to the lake is more variable than nitrate supply, both in time and source.

The contribution of inflow phosphorus to the lake area will be discussed as a "loading" in section 4.2.7.

3.1.2.2.3 Silica

Although considered as a minor element within a water body, silica may be present in large quantities. Like the other minor elements, it is of biological significance (Golterman, 1975a). The reactive silica reported in the present study was SiO_2. The mean values for each of the inflows are given in Table 3/4, with an overall mean for all inflows of 16.0 $g.m^{-3}$, and a range of 8.6 to 28 $g.m^{-3}$.

The individual inflows showed slight differences in mean concentrations. The slower flowing Hart's Creek, Halswell and LII had higher concentrations than the Selwyn River. This may be a response to the time required for the dissolution of silica by chemical weathering, where the slower flow rate of some rivers allow more time for this dissolution. The catchment at the Halswell River also includes part of the volcanic Banks Peninsula, which may contribute silicates to the inflows to the eastern side of the lake.

When the present levels of silica were compared with the levels reported for 1973-74, few changes were observable. The only sizeable change was a drop in concentration in the Selwyn River.

The contribution of inflow silica to the lake area will be discussed in section 4.2.7.

3.1.2.3 Trace Elements

The trace elements comprise several elements, mainly metals, found in small quantitites within a natural water body. Despite their

low levels, they are often essential to biological organisms (Golterman, 1975a).

Few analyses have been done on trace elements in the present study. Table 3/4 includes the available data, based on either 2 or 4 samples. Iron was analysed for each of the four inflows once, and this may be compared with the 1973-74 data. The Halswell has the highest level of iron, and this increased between 1973-74 and 1978. The other inflows had decreased iron levels over the same period.

Strontium was at twice the concentration in the LII River than in the Selwyn at the same time. Other elements, cadmium, copper, manganese and zinc all showed low levels (< 0.01 g.m^{-3}) for both LII and the Selwyn.

Little significance can be placed on these results for the trace elements. It is, however, important to recognise base levels for comparison, should changes in the catchment take place.

3.1.2.4 Dissolved Gases

The two dissolved gases of importance within the inflows are dissolved oxygen and carbon dioxide. Their solubility is influenced by temperature, partial pressure of the gas, and in the case of CO_2, also related to the bicarbonate system (Golterman, 1975b). Oxygen is produced by photosynthesis of algae and macrophytes within a river, and will therefore be subject to diurnal changes (Golterman, 1975b).

Table 3/4 gives the mean concentrations for each of these gases in each of the inflows, and the overall mean for the inflows. The mean carbon dioxide level was 4.2 g.m^{-3}, with a range from zero to 13 g.m^{-3}. The LII and Halswell both had higher levels, whereas the Selwyn had the lowest mean concentration. The overall mean concentration of dissolved oxygen was 9.2 g.m^{-3}, with a range from 6.1 to 12.8 g.m^{-3}. The individual inflows showed slight variation, with the lowest mean that of the LII at 8.49 g.m^{-3}, and the highest was the Selwyn, at 10.01 g.m^{-3}.

Compared with the results of the 1973-74 survey (Table 3/4), there is little change. The means for oxygen are extremely close, whereas the carbon dioxide levels are slightly higher in each inflow.

This slight change in carbon dioxide would account for the corresponding decrease in pH (section 3.1.2.6.1).

3.1.2.5 Organic Compounds

The only direct measurement of organic compounds was the analysis of total organic nitrogen. However, an organic component is included within the total phosphorus analysis (see Golterman, 1975a: p.87 footnote).

The levels of organic nitrogen within the inflows are given in Table 3/4. The overall mean concentration was 0.375 $g.m^{-3}$. The mean levels within the individual inflows are also very variable. The highest levels are found in the Halswell, and the lowest levels in Hart's Creek. Although lower than the nitrate levels, they are considerably greater than the combined input from nitrite and ammoniacal forms. This will be discussed in greater detail when the nitrogen cycle within the lake is considered (section 4.2.3.1).

Compared with the organic nitrogen levels recorded in 1973-74, the levels are lower. In all the inflows, there has been a large decrease in the intervening period. The overall mean value shows a 61% decrease, although the Halswell has only a 21% decrease. No explanation is offered to account for this decrease, but it must also be remembered that in the same period an even larger increase of inorganic nitrogen has been recorded (section 3.1.2.2.1).

3.1.2.6 Other features of importance

In the preceding sections on the composition of the inflows, reference was made to other important features. These measures are not due to one chemical species, but rather a combination of components, either dissolved or particulate. Total hardness, although measuring more than one ion, has already been discussed. Other features included in this section are pH, conductivity, suspended solids and absorbance.

3.1.2.6.1 pH

The regulation of pH in a natural water body is by a series of equilibria within the calcium bicarbonate system. Stumm and Morgan (1970), Golterman (1975a,b), and Moss (1980) discuss the detailed chemistry of this system. The important features are the relative

insolubility of calcium carbonate and the solubility of carbon dioxide in water. The pools of inorganic carbon are in the form of CO_2 and HCO_3^- which depends on the H^+ concentration, of which pH is a measure.

The pH measurements for the inflows have an overall mean of 7.4 with a standard error of 0.033 (Table 3/4). The individual inflow means range between 7.2 and 7.5 . These levels are comparable with the 1973-74 measurements, except in the Halswell and LII, where pH has declined. This decline corresponds to an increase in free carbon dioxide within the inflows.

The graph of pH over the two-year period (Figure 3/7A) shows a definite seasonality. The pH values increased in the inflows in spring of both 1978 and 1979, and declined during mid-summer (December-January). There was also a noticeable difference in the overall levels in each of the two years. Thus, it is possible that the decline noted between 1973-74 and 1978 may be due to seasonal differences, rather than an overall trend in the pH levels.

3.1.2.6.2 Conductivity

Electrical conductance (conductivity) is a measure of the ability of a conductor to convey electricity (Golterman et al. 1978). Differences in the conductivity of water samples are mainly a result of differences in the concentration of charged solutes and to an extent, the nature of the solutes and temperature.

As was noted earlier (section 3.1.2.1) the river samples were collected closer to the lake than in the 1973-74 survey. On several occasions, which coincided with high lake levels, conductivities were higher than expected. This was especially so of the Selwyn and Halswell Rivers. As a consequence, five conductivity measurements have been deleted (samples 2/03, 22/09, 23/09, 24/09 and 26/09) so that the data presented gives an accurate indication of inflow conductivities.

The mean conductivity for the inflows was 21.4 $mS.m^{-1}$ (Table 3/4), with a range 7.7 to 39.2 $mS.m^{-1}$. The individual inflow means range from 13.8 to 28.1 $mS.m^{-1}$. The Halswell had the highest conductivity and the Selwyn (after rejection of the listed samples) had the lowest. This general trend is in agreement with the concentrations of the ionic species, as reported previously (section 3.1.2.1).

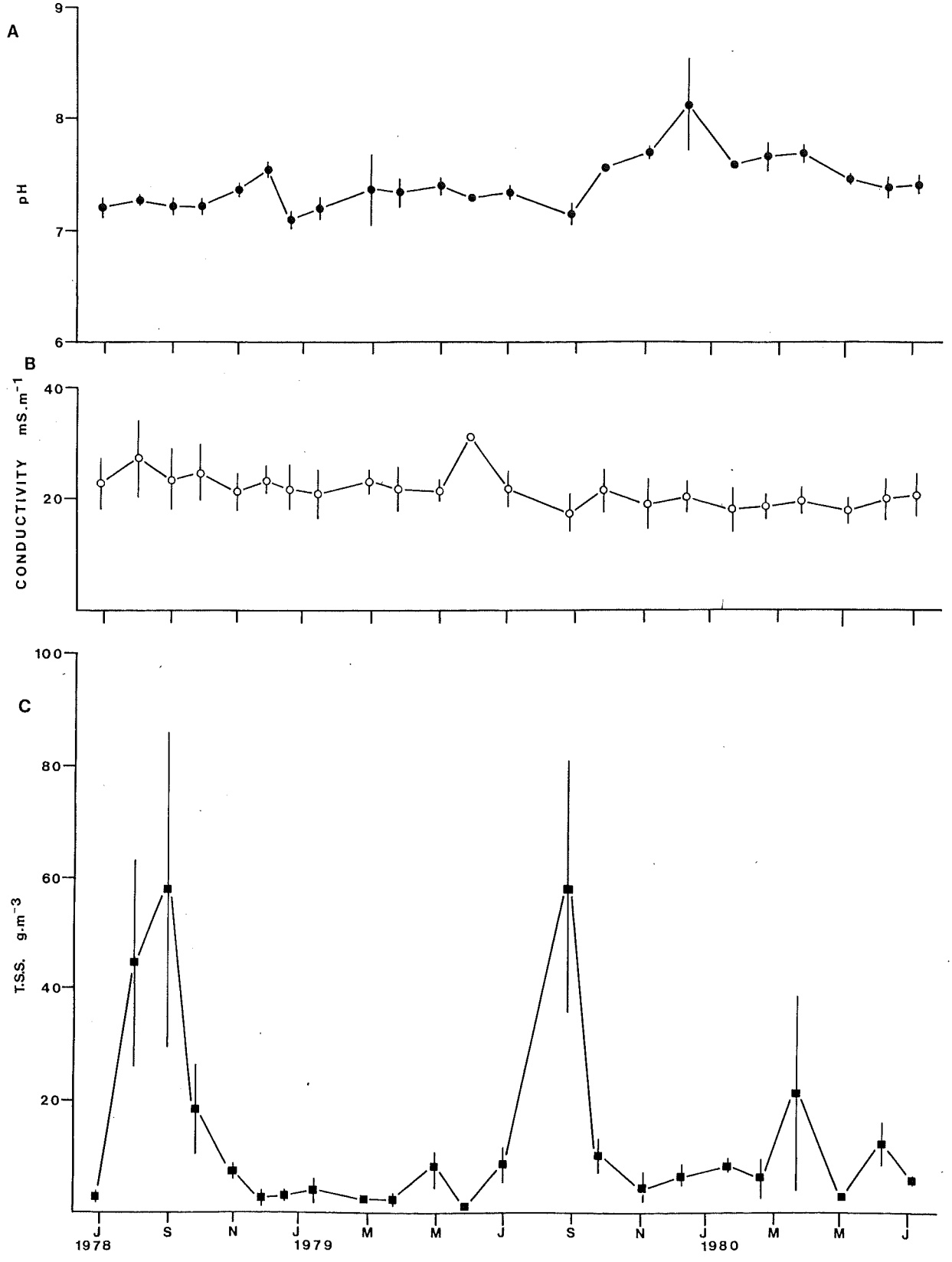


Figure 3/7: A. Mean pH of Inflows (±S.E.)
B. Mean Conductivity of Inflows (±S.E.)
C. Mean Total Suspended Solids in Inflows (±S.E.)

There is no seasonal pattern associated with conductivity (Figure 3/7B). After deletion of the spurious results, the graph shows the constancy of the inflows. The one point that is higher occurred during May 1979 (Collection 12), when only the Halswell was sampled. Consequently, this point is not a mean value (± standard error), but the actual record.

3.1.2.6.3 Suspended Solids

Suspended solid material within the inflows is a total measure of the particulate matter, whether it be organic or inorganic. Golterman (1975b) reviewed the definitions of the inorganic solids and mentioned the importance of particulate transport within rivers, especially silts. It was shown that ratios between dissolved and suspended compounds may be controlled by climate, relief and rock type.

The quantity of suspended solids within the inflow rivers to Lake Ellesmere varied considerably (Table 3/4). The mean quantity was 13.6 $g.m^{-3}$, with a range from 1 to 134 $g.m^{-3}$. The individual inflows can be grouped: the Selwyn and Halswell had a high sediment level, and the LII and Hart's Creek had lower levels. The levels as reported in this present context were at low flow periods (see section 3.1.1) and do not account for flood periods. No doubt during flood periods higher levels of suspended solids would be found.

The levels of suspended solids found during the 1973-74 survey were much greater than for the 1978-80 period. This change is not considered to be of importance, but rather reflects on the sampling method.

The graph of suspended solids with time (Figure 3/7C) shows a definite seasonality. Although these results do not indicate flood periods, it would appear from the graph that the inflows carried higher sediment loads during the winter periods. For both years during August-September the mean levels were much higher than for the rest of the year. Peaks in both flow rate and total-phosphorus (Figures 3/3A and 3/6A) occurred at the same time in 1979.

3.1.2.6.4 Absorbance

Absorbance measured at 270 nm is a measure of dissolved organic compounds within a filtered water sample. The more coloured the water, the higher the absorbance. This measure is approximately equal to Hazen units of colour, after multiplication by 100 (D.S.I.R., pers. comm). This index has been used little in the literature.

The absorbance levels with the inflows had a mean of 0.086, with a range up to 0.476 units. The individual inflows showed distinctive differences, however. The Halswell had the highest mean absorbance, at 0.168 units, and all the other means were at least half this level.

Little further use can be made of this data since no comparative measures can be found in the literature. It is expected that these values would be relatively low, especially compared with other brown-water humic lakes in New Zealand. The water within the inflows was not noticeably coloured on most occasions, except for the Halswell.

3.1.3 Discussion of Inflows

From the data presented on the four major inflows into Lake Ellesmere, it is possible to note patterns and trends.

The Halswell River has the highest levels of the major ionic elements, trace elements, plant nutrients, organic compounds and sediment content. However, when its flow rate is considered, the mass-flow analysis (section 3.1.2.2) is a more useful measure of input into the lake. The mass-flow of soluble-phosphorus from the Halswell River is high and comparable to that of the LII. However, the mass-flow of nitrate from the Halswell is low. On the other hand, the Selwyn has lower levels of many elements and nutrients, yet it has the highest flow rate. This results in the highest mass-flow rate for nitrate and total phosphorus of any of the rivers.

The other two major inflows, the LII and Hart's Creek have ionic and nutrient concentrations between those of the Halswell and Selwyn. The few exceptions include the lower dissolved oxygen level in the LII and lower nitrite-nitrogen, ammoniacal-nitrogen, total organic nitrogen and total-phosphorus in Hart's Creek.

The plant nutrients showed no definite seasonal fluctuation. Soluble-phosphorus in the inflows exhibited a delayed response to

rainfall, which was very variable over the period (section 3.1.2.2.2); whereas total-phosphorus was more closely related to the sediment load of each inflow. Inorganic nitrogen had no such response.

Comparisons with previous data illustrated some important changes in the inflows. Since the survey of 1973-74 there had been an increase in plant nutrients, especially nitrate and total-phosphorus. Other increases were noted in trace elements, and slight decreases in organic nitrogen and soluble phosphorus.

Further analysis of the relationships between inflow variables and the lake will be found in the nutrient loading data (section 4.2.7).

3.2 OUTFLOW

The outflow to Lake Ellesmere is neither permanent nor natural at the present time. Although there have been several attempts to establish a permanent opening in the past, they have all failed. The site where openings are made is the place which would be a natural opening if the water-level were allowed to rise sufficiently. This site is at the south-west corner of the lake, on the spit opposite the settlement of Taumutu. The artificial breach of the spit is made when the level of the lake reaches predetermined levels (Dwyer, unpublished, 1980).

The opening may be started when the level is rising near the target so that given favourable conditions, the actual opening will occur before the target is reached. During rough weather conditions, an effective opening may be difficult to make. In good weather with calm seas, little wind and high lake level (giving a high pressurehead) an opening made with bulldozers and dragline would develop quickly and remain open almost indefinitely. However, in bad weather, when seas would be rough and lakewater would probably be 'blown' away from the opening site, an opening would be difficult to develop, and would be unlikely to last very long (Dwyer, unpublished, 1980).

The present method of opening has been carried out by the North Canterbury Catchment Board since 1947, when it assumed responsibility for the lake level control. The maximum water levels for the lake are set by regulation according to the times of year. During the summer, September to April, the maximum water level is 1.05 m (3.45 ft) above

mean sea level and during the winter, May to August, the maximum level is 1.1 m (3.7 ft) above sea level (Dwyer, unpublished, 1980). If the lake was not artificially opened at these water levels, large areas of adjacent land would be flooded periodically (see section 4.1.1).

3.2.1 Lake Openings

The number and times of lake openings during 1978-80 are given in Table 3/8. Only those openings which lasted more than four days are recognised as effective (N.C.C.B., pers. comm.). During the three years 13 openings were made, compared to the average of 3.17 per year for the period 1947-1970 reported by Dalmer (1970) and Hughes et al. (1974). The previous mean length of opening was 24.2 days, whereas the mean opening time for 1978-80 was 25.1 days.

This higher number of openings is critical for the lake system. It will be shown (section 4.1.2.1) that seawater influxes occurred at several openings during the study period, as was particularly evident during the long opening of November 1979 to January 1980. The resulting increase in salinity had an effect on the lake flora (see chapter 6).

3.2.2 Hydrological and Chemical Output

The only hydrological data associated with the outflow from Lake Ellesmere is from an opening made on 5 July, 1972 (N.C.C.B., pers. comm.). Gaugings were made during the discharge at different times during the day. Table 3/9 gives the mean velocity and discharge for one day a week after the opening was made. It ranged from 153.8 to 176.5 $m^3.s^{-1}$.

This rate of discharge is not maintained after the water level in the lake drops. After sometime, if the shingle is not moved to close the artificial breach, part of the lake may become tidal.

In hydrological terms, this input may make little difference but chemically it has a drastic effect upon the lake, due to the higher salinity of the inflowing water.

The chemical and biological nature of the outflow water is unknown. It is possible to assume however that it would resemble the lake water at the south-west corner of the lake (close to Site 13) just prior to opening.

Table 3/8: Lake Openings, 1978-1980.

Year	Date Opened	Date Closed	No. days open
1978	April 25	May 24	29
	July 18	August 17	33
	September 5	October 4	29
	October 31	November 9	9
	December 18	January 3	16
1979	April 6	April 16	9
	May 23	June 7	15
	August 13	September 30	48
	November 4	January 18	75
1980	April 11	April 22	11
	May 13	May 31	18
	August 9	August 19	10
	September 11	October 5	24

Source: NCCB, pers. comm.

Table 3/9: Outflow Discharge after being open for one week.

5 July 1972

Time Hours	Width m	Mean velocity $m.s^{-1}$	Discharge m^3s^{-1}
1145-1230	46	1.82	153.8
1335-1405	46	2.13	176.5
1430-1505	46	2.16	175.2

Source: NCCB, pers. comm.

A study of a scale model of the lake has shown the general pattern of flow resultant from the opening of the lake (Gunthorp et al., unpublished, 1972). The pattern of flow caused a current across the lake from the Kaituna end towards the Selwyn, before discharging through the outflow. The pattern was little affected by the introduction of a shaped sand bottom. The embayments on either side of the Selwyn delta, the Kaituna and beyond the Halswell River mouth, and north of Garibaldi Island on the western margin effectively became backwaters. Although these results were observed in a physical model of the lake, they are consistent with data to be presented in the next chapter on the lake environment (section 4.2.1). It will be shown that the embayment to the west of the Selwyn delta differed from the pattern of ionic composition for the rest of the lake.

3.2.3 Discussion of the Outflow

The limited supply of data on the outflow from Lake Ellesmere has restricted the scope of this discussion. Very little more than the number and times of openings is known about this highly man-modified outlet from the lake. The physical resources required to measure the quality of the outflow on the irregular occasions when it was opened made further measurements impracticable.

This lack of data has, however, important ramifications in terms of a more detailed limnological knowledge of the lake. Three features can be identified as important for this study. They are the irregularity of opening, the volume decrease of the lake and the likelihood that influx of seawater will occur.

The irregularity of opening is due to the basis on which the decision to open the lake is made. During wet seasons (winter, and some summers), more openings are made, and the lake is thus drained more often. The irregularity of opening is also of importance in terms of life cycles of sea-run species of fish within the lake (Hughes et al., 1974).

The volume decrease of the lake caused by openings is important in terms of light-climate within the lake, and the dilution effect of the inflows. The light penetration of the water and potential light limitation will be discussed in terms of the mixed depth to euphotic depth ratio (sections 4.2.6.2). When the lake level is high, this value will be greater and light restriction will be greater than at times of low water. More importantly, the effect of the inflows

replenishing the lake after an opening will be very different from the dilution of a full lake. This will be noted in relation to the nutrient loading concept (see section 4.2.7), and in terms of the dilution of the seawater content at the lake with the freshwater of the inflows.

The third important character of the outflow is the seawater influx when the lake level is lowered. This will be shown to have an important effect on the composition of the lake (see section 4.2.1).

3.3 CLIMATE

Apart from the inputs to the lake system by the direct inflows, the climate of the lake environment and catchment also makes an important contribution to the system.

The climate in the vicinity of Lake Ellesmere is influenced by the Canterbury plains, the Pacific Ocean and Banks Peninsula. De Lisle (1969) has discussed the Canterbury climate and shown the overall importance of the westerly wind system, and the distinctive features produced to the lee side of the Southern Alps.

The predominant air circulation pattern is of anticlockwise anticyclones, with associated troughs which move across the Tasman Sea on to the South Island (de Lisle, 1969). As the air is forced over the Alps, it produces a föhn wind, the nor'wester. This is a strong turbulent wind which often reaches across the plains to the sea, bringing high temperatures and low humidity. A strong north-west wind which has been forced around the Alps and leaves Cook Strait comes under the action of a pressure gradient, directed towards the lee of the Alps. This gives the second important feature of the Canterbury climate, a cool north or north-east wind off the sea. This is developed and funnelled by the hills of Banks Peninsula and influences the Ellesmere district.

Another important wind is the coastal sea breeze which blows in all seasons except winter (de Lisle, 1969). If other winds are light, the sea breeze may develop early in the day, especially where the plain is wide, due to the relative heating effect of the land.

The production of rain in lowland Canterbury is not usually due to the northwest wind, but rather to the passage of a depression and a south-west air-flow (de Lisle, 1969). Even at such times, the

amount of the rainfall is low compared with many other areas in New Zealand.

The closest meteorological station to Lake Ellesmere is at Lincoln College, about 9 km from the lake. This station has been operated since 1944, before which a comparable station was operated at Lincoln township. From a compilation of records from the College site (43°39'S, 172°27'E) and the previous location at Lincoln township (43° 39'S, 172° 28'E) climatic data is available back to 1881 (New Zealand Meteorological Service, 1973).

The climatic records for the sampling period, June 1978 - July 1980 will be compared with the long term records to establish the peculiarities of this period. The comparison will be based on mean monthly records in the present section, because of the form of the available data. In subsequent discussions, time periods related directly to sampling dates will be used (as described in Chapter 2, Table 2/5). In this manner a direct pattern of influence on the lake can be established.

3.3.1 Rainfall

The rainfall levels as recorded at Lincoln College may be lower than those at the seaward side of Lake Ellesmere. However, the pattern and trends at the college should reflect the situation at the lake to some degree.

The mean monthly rainfall figures for Lincoln have a seasonal pattern and include a low spring rainfall and higher levels in autumn and winter. The range is from 46 mm in September to 76 mm in May (Table 3/10, Figure 3/11A). This rainfall mostly falls on 7 - 9 days of each month.

The mean monthly rainfall over the 1978-80 period diverged widely from the average mean monthly rainfall figures (Figure 3/11A). During the winter of 1978, the levels were above the mean with a peak in July twice the normal fall, at 112 mm. From spring 1978 to the end of 1979 there were large monthly oscillations of rainfall, with the recorded values both above and below the appropriate mean values. These oscillations were generally regular in occurrence. If one month was unusually dry, the next month was unusually wet. During this period, two months (April and June 1979) were the driest on record

Table 3/10: Summary Climatic Observations, Lincoln College.

	J	F	M	A	M	J
Rainfall, mm Normal 1941-1970	56	56	66	58	76	58
Temperature, °C Normal 1931-1960	16.0	15.8	14.1	11.4	8.1	5.6
Wind Run, km Daily Windrun 1964-1970	327	325	288	293	251	222
Sunshine, hours % of possible 1935-1970	48	48	46	44	42	43
Average per day 1935-1970	7.16	6.62	5.68	4.77	3.94	3.80

	J	A	S	O	N	D	Year
Rainfall, mm Normal 1941-1970	58	56	46	48	53	58	689
Temperature, °C Normal 1931-1960	4.8	6.4	8.5	10.9	12.8	14.8	10.8
Wind Run, km Daily Windrun 1964-1970	230	254	296	323	311	323	287
Sunshine, hours % of possible 1935-1970	42	46	48	49	48	46	47
Average per day 1935-1970	3.84	4.68	5.53	6.39	6.97	6.94	

Source: N.Z. Met. Service (1973).

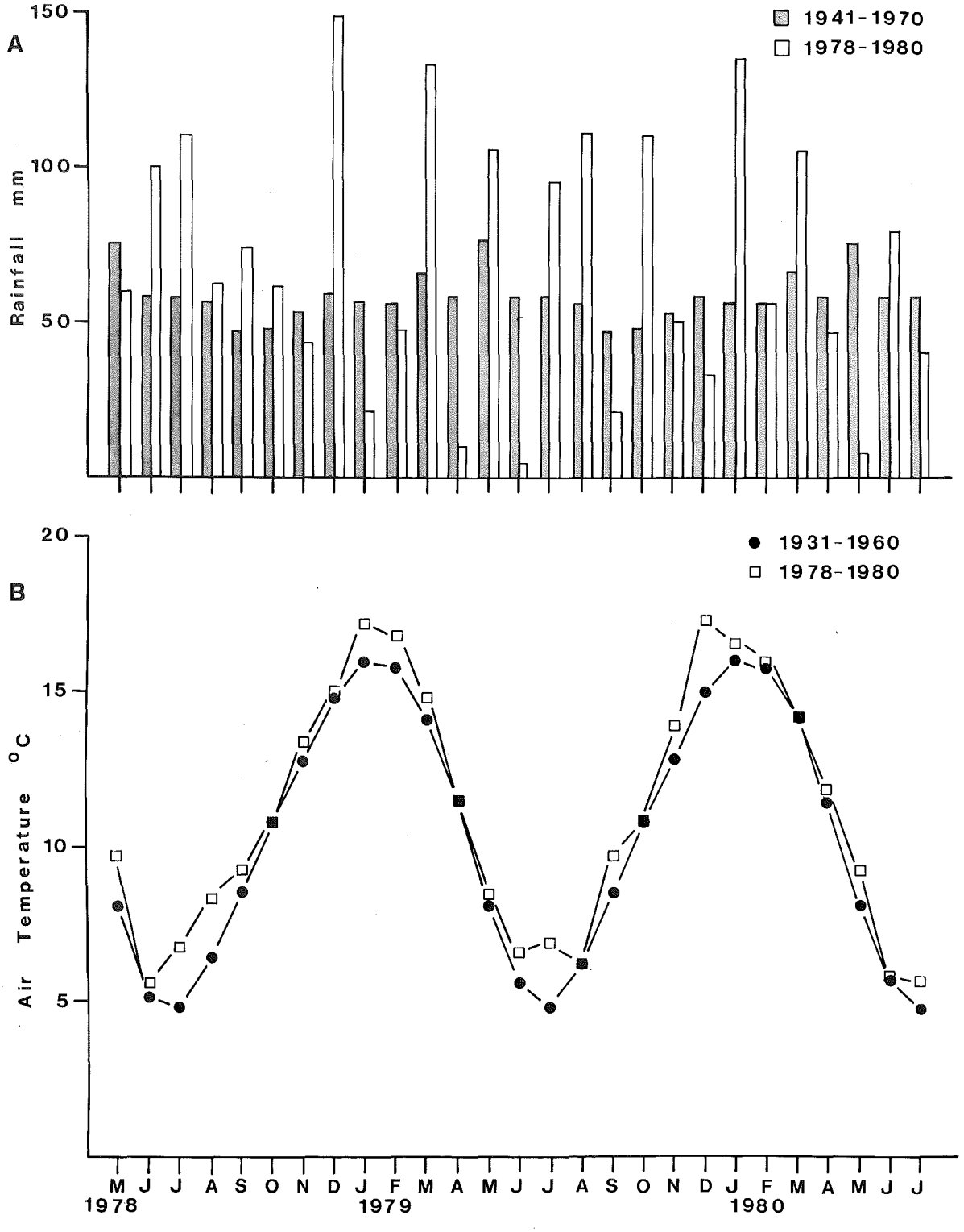


Figure 3/11: A. Mean Monthly Rainfall, 1978-1980; Long-term Mean, 1941-1970.

B. Mean Normal Air Temperature, 1978-1980; Long-term Mean, 1931-1960.

since 1881. The summer period of 1979-80 (January-March) had high rainfall and was followed by a drier than average autumn period. This dry period included another "driest on record" month for May.

3.3.2 Air Temperature

The mean normal air temperature records for Lincoln College are based on the period 1931 - 1960. It is calculated as (½ (mean max. + mean min.)). The range is from the winter low of 4.8°C in July to a high of 16.0°C in January (Table 3/10). The daily range in temperature varies little throughout the year, although there is a slight seasonal influence. In July the daily range is 9.1°C, whereas in November and January the range is 11.4°C.

The 1978-80 period is compared with the mean normal temperatures in Figure 3/11B. Over the whole sampling period the air temperatures were above normal, especially during December 1979. During this month the temperature was 2°C warmer than the mean expected temperature.

3.3.3 Wind

Wind is an important factor in the Ellesmere district because of the flat, exposed nature of the landscape, and the shallowness of the lake itself. De Lisle (1969) has reported the highest winds in the whole of Canterbury were at Ellesmere. The present study is based on the data recorded at Lincoln College using two different approaches. Mean daily windrun gives some idea of windiness over the whole period, whereas wind force gives some indication of intensity. Discussion of the effects of wind action on the lake is included in a later section (4.2.6.2).

The mean daily windrun taken over a month (Table 3/10) indicates the overall amount of wind for a given day. The long-term mean values (1964-1970) are shown in Figure 3/12A. The general pattern found is seasonal, with high summer windrun, and less total wind in the winter. Over the period 1978-1980, the mean daily windrun was higher than this average (Figure 3/12A). Only in the autumn of 1980 was the level lower than the mean for any length of time.

A second approach is presented in Figure 3/12B where the strength of the wind is presented as the number of days per month with wind of a given force. When assessed in the Beaufort scale, only two days had strength of greater than or equal to 8 during the

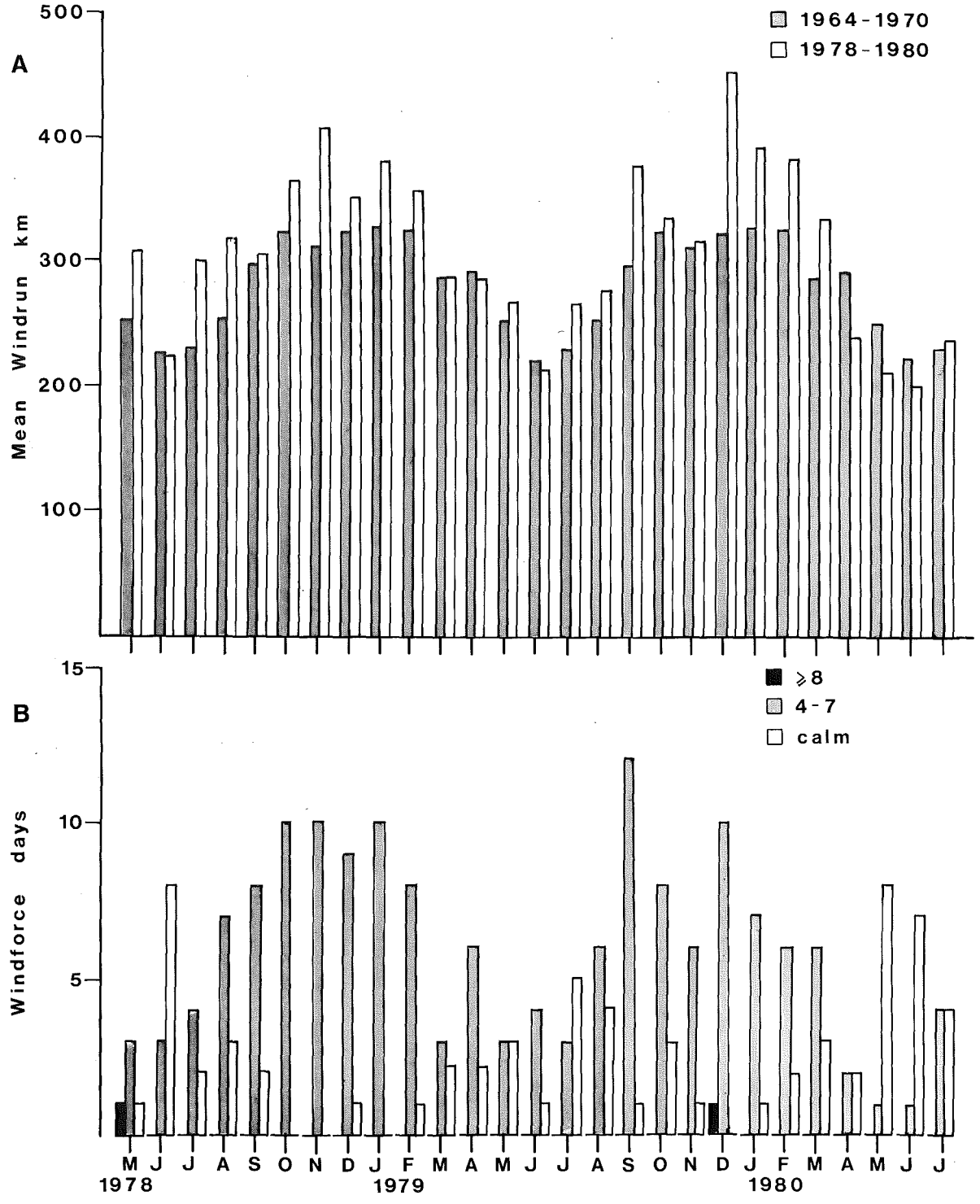


Figure 3/12: A. Mean Daily Windrun for Month, 1978-1980; Long-term Mean 1964-1980.

B. Number of days of Windforce of various strengths (Beaufort scale).

whole of the sampling period. However winds of force 4 to 7 were frequent. There is some seasonality expressed, for more days per month in late winter and spring had moderately strong winds than did days in the autumn-early winter period. Calm days were correspondingly higher in number in early-winter periods than in spring periods.

The differences between the two methods of analysis of wind (total windrun and wind strength) can be easily reconciled. Total windrun was an integrated measurement over the whole day and recorded at 9 a.m., whereas the strength of wind was assessed only at 9 a.m. for that day. As a consequence, coastal winds, which tend to arise later in the day (see 3.3 introduction) are more significant in the total windrun measurements.

3.3.4 Sunshine and Cloud Cover

Sunshine hours and the extent of cloud cover are inversely related. However, this may not be obvious from the figures. Sunshine is assessed as a total for the day, whereas the cloud cover is only assessed at 9 a.m. each day.

The mean expected sunshine hours have been calculated from the percentage possible hours, and expressed as a mean per day (Table 3/10). This takes account of the variable lengths of months. It can be noted in passing that bright sunshine hours at Lincoln are consistently less than 50% of possible hours. The mean expected value is graphed along with the mean over the 1978-80 period (Figure 3/13A). The daily mean ranged from 3.8 to 7.2 hours. As would be expected, there is a distinct seasonality due to the temperate latitude of the Ellesmere district. The period 1978-80 followed the mean expected value for much of the time. However, departures from the mean were evident in March 1979, when the mean daily sunshine was 2.2 hours less than average.

The mean daily cloud cover for the 1978-80 period is presented in Figure 3/13B. Although long-term means are not available, some peaks are noteworthy. The month of March 1979 had the highest mean cloud cover, at over seven-eights cover. Other cloudy months were September and October 1979. This period corresponded to the lower than average sunshine hours found in Figure 3/13A.

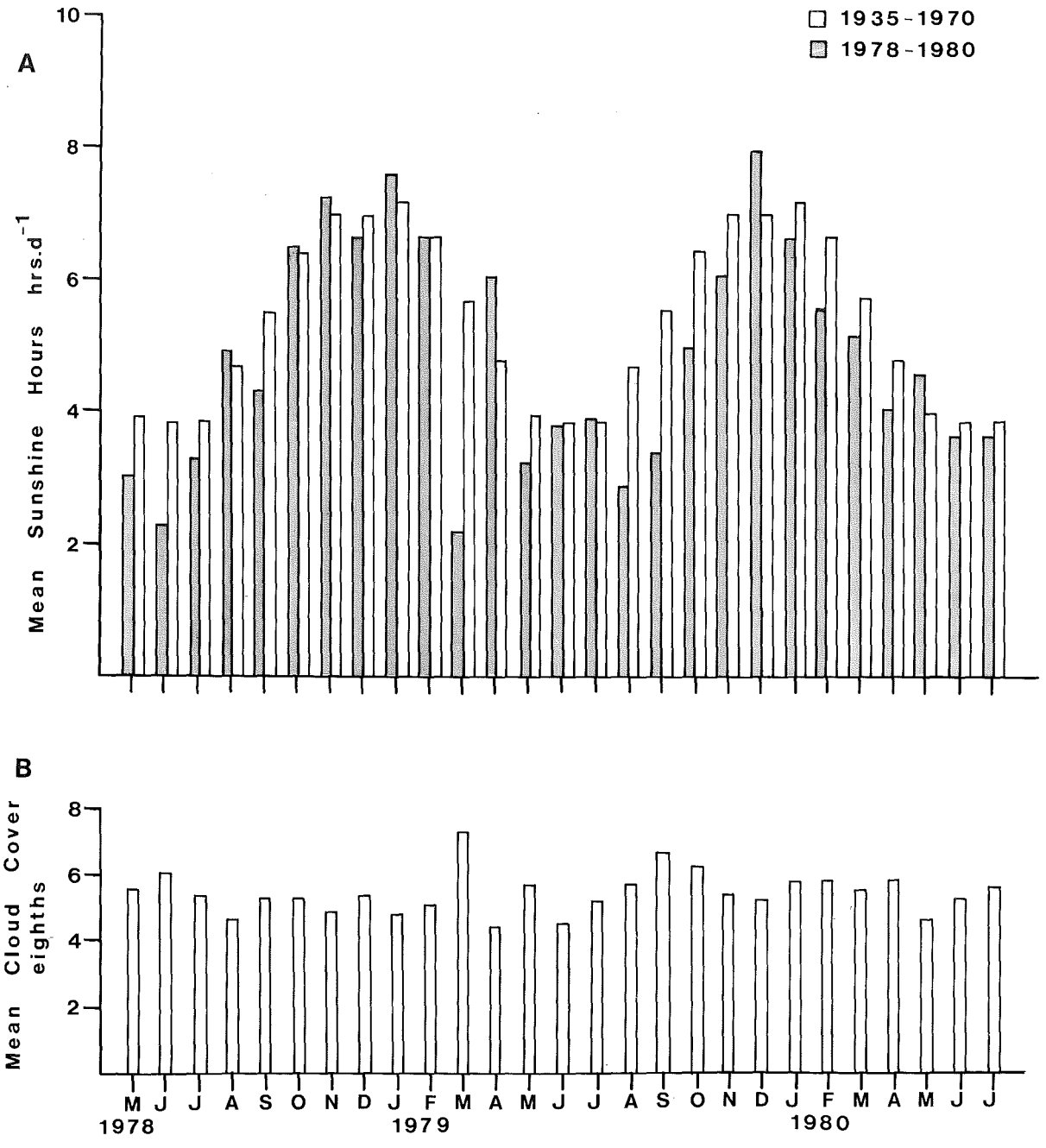


Figure 3/13: A. Mean Daily Sunshine Hours, 1978-1980
Long-term Mean 1935-1970

B. Mean Daily Cloud Cover, 1978-1980.

3.3.5 Discussion of Climate

The sampling period, 1978-1980 has been compared with long-term means and several climatic trends are noted. Over this period there have been times of lower than average sunshine hours especially in 1979 and early 1980. Rainfall was heavy in the winter of 1978 and distinctly variable in 1979 and 1980, and several months in this period were the driest on record (e.g. April and June, 1979; May 1980). Overall, the period May 1978 to July 1980 was warmer and windier than the average for that area.

CHAPTER 4

LAKE ENVIRONMENT

This chapter discusses the environment of Lake Ellesmere in physical and chemical terms. This will enable the phytoplankton population ecology to be interpreted at a later stage. Prior to this study there was a scarcity of available data on the lake. Before the comparable 1973-74 survey of the lake, chemical data was based on sporadic samples for chloride, phosphorus and nitrogen concentrations. These were collected from different parts or unrecorded sites within the lake, and have been summarized in Hughes et al. (1974). The 1973-74 survey by the DSIR has gone largely unreported, but provides a comparable data set to the present study. However sites sampled during that period were all close to the edge of the lake, and usually directly out from the inflows. The hydrological records of water level and lake openings have been made more consistently than the chemical records. Other factors such as bathymetry are entirely lacking.

4.1 HYDROLOGY AND PHYSICAL ATTRIBUTES

The physical environment of Lake Ellesmere has been described in part by Hughes et al. (1974) and Irwin (1975), and records of water level fluctuations have been made in recent years by the North Canterbury Catchment Board (pers. comm.).

The area of the lake varies with the height of the water. This is more noticeable than in many other lakes because of the gentle slope of the surrounding land. Irwin (1975) gives the area as 181.75 km^2, at the 3.25 ft (0.99 m) contour. Table 4/1 shows the area of the lake at other contour levels, and also the levels at which the lake is opened in winter and summer periods. No accurate estimate of the size of the lake is available, due to confusion over a reference datum level. Harris (1947) suggested Langbein's (1932) datum level was 9 inches above the mean sealevel. Hughes et al. (1974) give an area 2,000 acres smaller than that given by Langbein for the 1 foot contour, but the source of data used by Hughes et al. is unknown. The present

Table 4/1: Area of Lake at various contours.

Height a.m.s.l m	ft.*1	Area km^2	acres*1	Source
2.75	9	305.66	75,000	Norton,1980
1.43	4.7	228.78	56,510	Dick and Norton, 1954
	4	218.62	54,000	Langbein, 1932*2
1.1*3	3.7	211.37	52,210	Dick and Norton, 1954
1.06	3.5	202.42	50,000	Hughes et al., 1974
1.05*4	3.45			
0.99	3.25	181.75	44,892	Irwin, 1975
0.92	3	198.38	49,000	Langbein, 1932*2
0.61	2	182.18	45,000	Langbein, 1932*2
0.3	1	165.99	41,000	Langbein, 1932*2
0	0	153.84	38,000	Langbein, 1932*2

*1 calculated for comparison 1 ft. = 0.305 m.; 1 km^2 = 100 ha = 247 acres

*2 Harris (1947) suggests Langbein's datum level may have been 9 inches above mean sea-level, thus affecting all the areas recorded.

*3 maximum water level in winter before opening.

*4 maximum water level in summer before opening.

day area of the lake is substantially smaller than a century ago (see section 1.2).

The maximum length of the lake is 26.3 km in the ENE direction and maximum width is 12.9 km (Irwin, 1975).

4.1.1 Bathymetry

The detailed bathymetry of Lake Ellesmere is unknown but the lake is very shallow. Its maximum depth is approximately 2.1 m (7 ft) below mean low-water level (Irwin, 1975). Langbein (1932), however, notes the maximum depth as only 6 ft below mean sea-level. Harris (1947) gives a mean low-water at Lyttelton as 2.91 feet below mean sea level. Therefore the maximum depth of the lake is about 3.02 m (9.91 feet) below mean sea level, or 4.01 m (13.16 feet) below the 3.25 foot contour as shown on the NZMS 1 series, S93.*1

Hughes et al. (1974) give the mean lake depth at mean sea level as 2.1 m (7 ft). No source is given for this figure and it cannot be confirmed. However there is a curious similarity between the maximum depth given by Irwin (1975) and the mean depth given by Hughes et al. (1974).

The lake margin is very gentle in slope. Assuming that the gradient of the surrounding land continues to the centre of lake, a small change in the height of the water would give a large change in the water capacity.

During the period of sampling, several sites off from the shore were found to be shallow, especially those along the western margin of the lake. For example, Site 12 (see Figure 2/2) was approximately 1 km off-shore, but when the lake was less than 0.58 m above mean sea level there was less than 1 m of water at this site (Collection 21, 22 January 1980).

The depth of the lake at any place and time is also affected by the wind. Langbein (1932) in a detailed comparison of water gauges showed that in a 100 $km.hr^{-1}$ (= 63 $mi.hr^{-1}$) southerly gale, there was a 0.5 m (= 20 inch) rise in water level at the northern end of the lake.

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*1 New Zealand Map Series 1: topographical maps, scale 1: 63360

Dalmer (1970) compared water level recorders at Taumutu and Kaituna and found they rose by up to 1 m (3 feet) during a south-westerly storm. During a storm in April 1968, the lake was raised by 1.2 to 1.5 m (4-5 ft) at the eastern end. The effect on the rest of the lake must therefore be considered during these times of severe weather.

4.1.2 Volume and Water Residence Time

The exact volume of Lake Ellesmere is not known, but estimates have been made in the past by Langbein (1932). The preceding discussion, however, indicates the problematic nature of all such estimates. Table 4/2 gives the estimated lake volume at various contour levels within the normal range of variation of lake height. These volumes have been calculated from the maximum lake depth, and the mean lake depth as previously discussed (section 4.1.1). Comparison of these estimated volumes shows that a change in depth of 0.76 m produces a change in volume of approximately 1.6 times.

Water residence time cannot be accurately determined for Lake Ellesmere because the total inflow into the lake is not known (section 3.1.1); the outflow data is largely unknown (section 3.2); and the volume of the lake has only been estimated within maximum limits. From the above calculations, however, the water residence time is expected to be in the order of months, rather than years.

4.2 LAKEWATER COMPOSITION

The composition of the lakewater is given in Table 4/3, based on 31 variables. The arrangement of this section is similar to that on inflows (section 3.1.2) and follows Golterman (1975a). The eleven sites within the lake were visited over the period June 1978 - July 1980, as outlined in section 2.2.1.

Previous chemical analyses were carried out in 1973-74 and these have gone largely unreported (D.S.I.R., pers. comm.). Although the mean results of this earlier survey are included in Table 4/3 it is not possible to discuss in detail the individual samples. Comparison will be made of mean values where significant trends are observed.

Table 4/2: Estimated Lake Volumes.

Contour level m	Area[*1] km^2	Max. Depth[*2] m	Mean Depth[*3] m	Est. Volume m^3
1.06	202.42	4.08		$<8.259 \times 10^8$
			3.16	6.396×10^8
0.99	181.75	4.01		$<7.292 \times 10^8$
			3.09	5.616×10^8
0.3	157.89	3.32		$<5.242 \times 10^8$
			2.4	3.789×10^8

Sources: [*1] Table 3/1

[*2] Irwin (1975), max. depth at mean low water

[*3] Hughes et al. (1974), mean depth at mean sea level

Table 4/3: Lakewater Composition (mean ±S.E.).*6

	Units	Sites*1 1	2	4
pH	-	8.58±0.08	8.48±0.09	8.31±0.13
salinity	‰	8.2±0.9	8.0±1.2	7.7±1.4
conductivity	$mS.m^{-1}$	931.4±106.7	942.9±119.1	816.5±132.4
total hardness	$g.m^{-3}$	1274±157	1238±182	1051±179
Major: Ca^{++}	"	61.7±3.5	61.6±6.0	49.7±4.4
Mg^{++}	"	143.3±14.5	135.7±13.9	109.3±10.6
Na^{+}	"	1266.1±108.0	1202.2±128.1	847.5±97.2
K^{+}	"	104.6±37.8	68.8±22.1	72.6±34.1
$CO_3^{=}$	"	9.4±2.2	9.8±3.2	8.9±3.1
HCO_3^{-}	"	67.0±2.7	70.5±3.2	71.8±2.9
CL^{-}	"	3634.4±428.7	3643.8±536.3	3174.5±614.4
$SO_4^{=}$	"	343.4±32.9	308.6±33.5	231.1±20.9
Minor: NO_3-N	"	0.482±0.098	0.406±0.106	0.748±0.172
NO_2-N	"	0.004±0.001	0.006±0.002	0.006±0.001
NH_4-N	"	0.007±0.003	0.007±0.003	0.022±0.007
Sol.-P	"	0.006±0.001	0.009±0.004	0.011±0.003
Tot-P	"	0.189±0.035	0.190±0.038	0.138±0.018
SiO_2	"	11.84±0.55	11.42±0.51	12.70±0.85
Gases: CO_2	"	0.385±0.158	0.423±0.168	1.217±0.417
diss.O_2	"	11.10±0.23	10.83±0.28	10.99±0.20
Organics: T.O.N.	"	0.935±0.137	0.975±0.097	1.147±0.102
Absorb.	-	0.097±0.007	0.104±0.008	0.137±0.016
Trace: Cadmium*2	"	<0.01	<0.01	<0.01
Copper*2	"	<0.01	<0.01	<0.01
Iron *3	"	0.04	0.04	0.10
Iron *2	"	0.05	0.05	0.05
Manganese*2	"	<0.01	<0.01	<0.01
Zinc*2	"	0.02	0.01	<0.01
Strontium*3	"			
Lithium*4	"			
Rubidium*4	"			
Fluoride*5	"			

Footnotes: *1For location of sites see Table 2/1.

*227.11.1978;

*326.6.1978;

*422.1.1980;

*526.9.1979.

*6This table appears on one page as Supplementary Table 2.

Table 4/3: Continued.

	Units	Sites*1 5	6	8
pH	-	8.45±0.10	8.27±0.13	8.33±0.13
salinity	‰	8.6±1.5	7.6±1.3	7.6±1.5
conductivity	$mS.m^{-1}$	945.9±135.3	819.1±132.4	732.1±136.2
total hardness	$g.m^{-3}$	1224±191	1003±189	961±184
Major: Ca^{++}	"	58.3±4.9	43.2±4.5	38.7±5.2
Mg^{++}	"	142.0±16.2	96.7±15.2	83.9±12.5
Na^{+}	"	1129.4±111.7	696.1±122.5	663.1±115.7
K^{+}	"	45.2±4.9	29.5±5.2	63.0±35.2
$CO_3^{=}$	"	9.6±3.0	9.2±3.3	7.2±1.7
HCO_3^{-}	"	69.7±3.0	63.6±3.1	60.3±3.3
CL^{-}	"	3679.3±626.8	2943.9±598.2	2841.6±610.0
$SO_4^{=}$	"	292.6±27.3	190.7±30.3	169.5±27.7
Minor: NO_3-N	"	0.489±0.983	0.947±0.220	0.970±0.181
NO_2-N	"	0.002±0.001	0.006±0.001	0.004±0.001
NH_4-N	"	0.004±0.001	0.033±0.009	0.016±0.006
Sol.-P	"	0.006±0.002	0.011±0.003	0.011±0.003
Tot-P	"	0.160±0.022	0.140±0.019	0.130±0.018
SiO_2	"	11.62±0.60	12.68±0.77	12.12±0.55
Gases: CO_2	"	0.591±0.170	1.087±0.361	0.783±0.259
diss.O_2	"	11.04±0.26	10.83±0.30	11.19±0.23
Organics: T.O.N.	"	1.017±0.136	0.915±0.133	0.876±0.102
Absorb	-	0.111±0.010	0.113±0.013	0.095±0.009
Trace: Cadmium*2	"	<0.01	<0.01	<0.01
Copper*2	"	<0.01	0.02	0.01
Iron {*3	"	0.12	0.12	0.38
Iron {*2	"	0.05	0.05	0.15
Manganese*2	"	<0.01	<0.01	0.02
Zinc*2	"	<0.01	<0.01	0.02
Strontium*3	"			
Lithium*4	"			
Rubidium*4	"			
Fluoride*5	"		0.21	

Table 4/3: Continued.

	Units	Sites*1 10	11	12
pH	-	8.45±8.11	8.47±0.10	8.53±0.11
salinity	‰	8.5±1.2	7.7±0.9	9.5±1.5
conductivity	$mS.m^{-1}$	842.5±128.7	871.6±107.4	981.0±126.4
total hardness	$g.m^{-3}$	1136±179	1158±150	1210±126
Major: Ca^{++}	"	48.0±4.8	51.7±5.3	58.9±6.1
Mg^{++}	"	117.0±13.4	123.4±19.6	150.2±21.8
Na^{+}	"	920.2±105.1	1026.0±140.5	1202.1±161.4
K^{+}	"	78.7±40.4	80.0±40.3	49.2±7.4
$CO_3^{=}$	"	8.6±2.1	8.3±2.0	10.2±2.5
HCO_3^{-}	"	64.7±2.8	63.9±2.63	64.5±3.5
CL^{-}	"	3279.5±580.2	3264.8±484.7	3723.1±552.7
$SO_4^{=}$	"	240.1±34.1	266.0±39.9	353.0±47.5
Minor: NO_3-N	"	0.841±0.211	0.719±0.135	0.609±0.139
NO_2-N	"	0.004±0.001	0.003±<0.001	0.004±0.002
NH_4-N	"	0.014±0.006	0.010±0.004	0.007±0.004
Sol.-P	"	0.010±0.002	0.011±0.003	0.012±0.003
Tot-P	"	0.127±0.014	0.155±0.031	0.127±0.019
SiO_2	"	12.96±0.50	11.48±0.48	12.08±0.58
Gases: CO_2	"	0.636±0.181	0.520±0.174	0.500±0.143
diss.O_2	"	11.23±0.29	11.43±0.26	11.69±0.34
Organics: T.O.N.	"	0.952±0.104	0.825±0.107	0.894±0.120
Absorb	–	0.096±0.007	0.093±0.006	0.092±0.009
Trace: Cadmium*2	"	<0.01	<0.01	<0.01
Copper*2	"	0.02	0.01	0.01
Iron {*3	"	<0.04	<0.04	<0.04
Iron {*2	"	0.05	0.10	0.15
Manganese*2	"	<0.01	<0.01	<0.01
Zinc*2	"	<0.01	<0.01	<0.01
Strontium*3	"			
Lithium*4	"		0.063	
Rubidium*4	"		0.13	
Fluoride*5	"			0.36

Table 4/3: Continued.

	Units	Sites[*1] 13	14
pH	-	8.54±0.10	8.50±0.10
salinity	‰	10.9±2.1	9.4±1.4
conductivity	$mS.m^{-1}$	1276.2±208.4	1005.8±135.8
total hardness	$g.m^{-3}$	1573±268	1288±185
Major: Ca^{++}	"	82.5±14.6	62.0±4.3
Mg^{++}	"	197.2±31.0	146.8±15.3
Na^{+}	"	2005.3±607.8	1179.9±99.8
K^{+}	"	99.0±28.7	48.0±5.3
$CO_3^{=}$	"	9.9±2.8	8.9±2.6
HCO_3^{-}	"	71.5±5.6	70.0±3.9
CL^{-}	"	5144.1±910.2	3895.8±617.9
$SO_4^{=}$	"	414.9±60.2	336.0±32.9
Minor: NO_3-N	"	0.447±0.111	0.393±0.106
NO_2-N	"	0.003±0.001	0.002±0.001
NH_4-N	"	0.011±0.007	0.008±0.004
Sol.-P	"	0.009±0.003	0.010±0.002
Tot-P	"	0.134±0.023	0.156±0.026
SiO_2	"	10.47±0.76	12.09±0.68
Gases: CO_2	"	0.909±0.496	0.545±0.183
diss.O_2	"	11.29±0.37	11.68±0.34
Organics: T.O.N.	"	0.851±0.139	1.118±0.202
Absorb	–	0.090±0.013	0.101±0.011
Trace: Cadmium[*2]	"	<0.01[*2&3]	<0.01
Copper[*2]	"	<0.01[*2&3]	<0.01
Iron {[*3]	"	0.11[*3]	0.09
Iron {[*2]	"	0.05[*3]	<0.05
Manganese[*2]	"	<0.01[*2&3]	<0.01
Zinc[*2]	"	<0.01[*2&3]	<0.01
Strontium[*3]	"	1.9[*3]	
Lithium[*4]	"	0.83	
Rubidium[*4]	"	0.18	
Fluoride[*5]	"	0.53	

Table 4/3: Continued

	Units	No cases	1978-1980 Mean	1978-1980 Range	1973-74 Mean
pH	-	256	8.453±0.034	7.2-9.5	8.3
salinity	‰	142	8.5±0.4	0.5-27.3	-
conductivity	$mS.m^{-1}$	255	922.7±40.5	26-4000	-
total hardness	$g.m^{-3}$	256	1192±56	80-5200	1070
Major: Ca^{++}	"	256	56.1±2.1	10-250	84
Mg^{++}	"	152	131.4±5.6	7-460	206
Na^{+}	"	152	1105.7±69.6	9-9550	-
K^{+}	"	152	67.5±8.4	3-563	-
$CO_3^{=}$	"	256	9.1±0.8	0-77	-
HCO_3^{-}	"	256	67.0±1.0	11-129	90
CL^{-}	"	256	3557.9±180.5	106-16700	3040
$SO_4^{=}$	"	151	285.3±12.0	24-875	450
Minor: NO_3-N	"	256	0.639±0.047	<0.010-3.750	0.15
NO_2-N	"	256	0.004±<0.001	<0.001-0.048	0.001
NH_4-N	"	256	0.013±0.002	0.001-0.160	0.013
Sol.-P	"	251	0.010±0.001	<0.001-0.086	0.008
Tot-P	"	244	0.151±0.008	0.013-0.960	0.16
SiO_2	"	256	11.94±0.191	1.3-22	16
Gases: CO_2	"	256	0.684±0.081	0-11	0.45
diss.O_2	"	144	11.20±0.08	8.7-14.3	10.3
Organics: T.O.N.	"	248	0.954±0.038	0.02-4.15	2.0
Absorb	-	245	0.103±0.003	0.014-0.319	-
Trace: Cadmium*2	"				
Copper*2	"				
Iron {*3	"				
Iron {*2	"				
Manganese*2	"				
Zinc*2	"				
Strontium*3	"				
Lithium*4	"				
Rubidium*4	"				
Fluoride*5	"				

4.2.1 Major ions and related measures

Moss (1980) argues that the major ions are not of importance in freshwater lakes except in very high concentrations. Lake Ellesmere has such a concentration, evidenced by the brackish nature of the water. The ionic composition of the lake is due to the proximity of the lake to the sea and subsequent sea-water influxes.

Table 4/3 gives the breakdown of the lakewater as a mean for each site, and an overall mean for the lake. In this table it is evident that sodium and chloride ions are present in highest concentration, which suggests some seawater influence. This was also reflected in the salinity and conductivity measurements. The overall mean salinity for the lake was 8.5 p.p.t. and the conductivity 9.22 $mS.m^{-1}$. This value was based on only 142 samples from collections 11 - 26. The measure of chlorinity gave a more complete picture because measurements were taken over the whole two-year period. The mean chlorinity for the lake was 3560 $g.m^{-3}$, which is 18.5% of the chlorinity of full seawater. At the time of openings into the sea, there was a higher mean salinity at some sites. Site 13 had the highest mean salinity at 10.9‰ (= p.p.t.), with sites along the spit margin having higher mean levels than those sites directly out from the rivers (sites 4,6,8: 7.7‰,7.6‰,7.6‰ respectively). Figure 4/4 shows the mean salinity values in the lake spatially and includes isograms of salinity. This map only indicates the sites tested and can therefore only provide an approximate indication of lake-wide salinity, but nevertheless, the centre of radiation is immediately evident.

This salinity is not just concentrated at the opening at Taumutu and in concentric rings about it, but is influenced by the spit margin. It is evident that salinity levels within the lake are a general consequence of seawater percolation through the shingle barrier between the lake and the sea. The brackish nature of the lake will be related to this percolation in a subsequent section.

The bay west of the Selwyn delta also had a high level of salinity. This bay has no major inflow and is something of a backwater. A similar area, into which the LII empties is to the east of the Selwyn delta. This area had a lower mean level of salinity. A generalized trend in salinity was evident between the outflow at the south-west corner of the lake and the freshwater inputs, especially

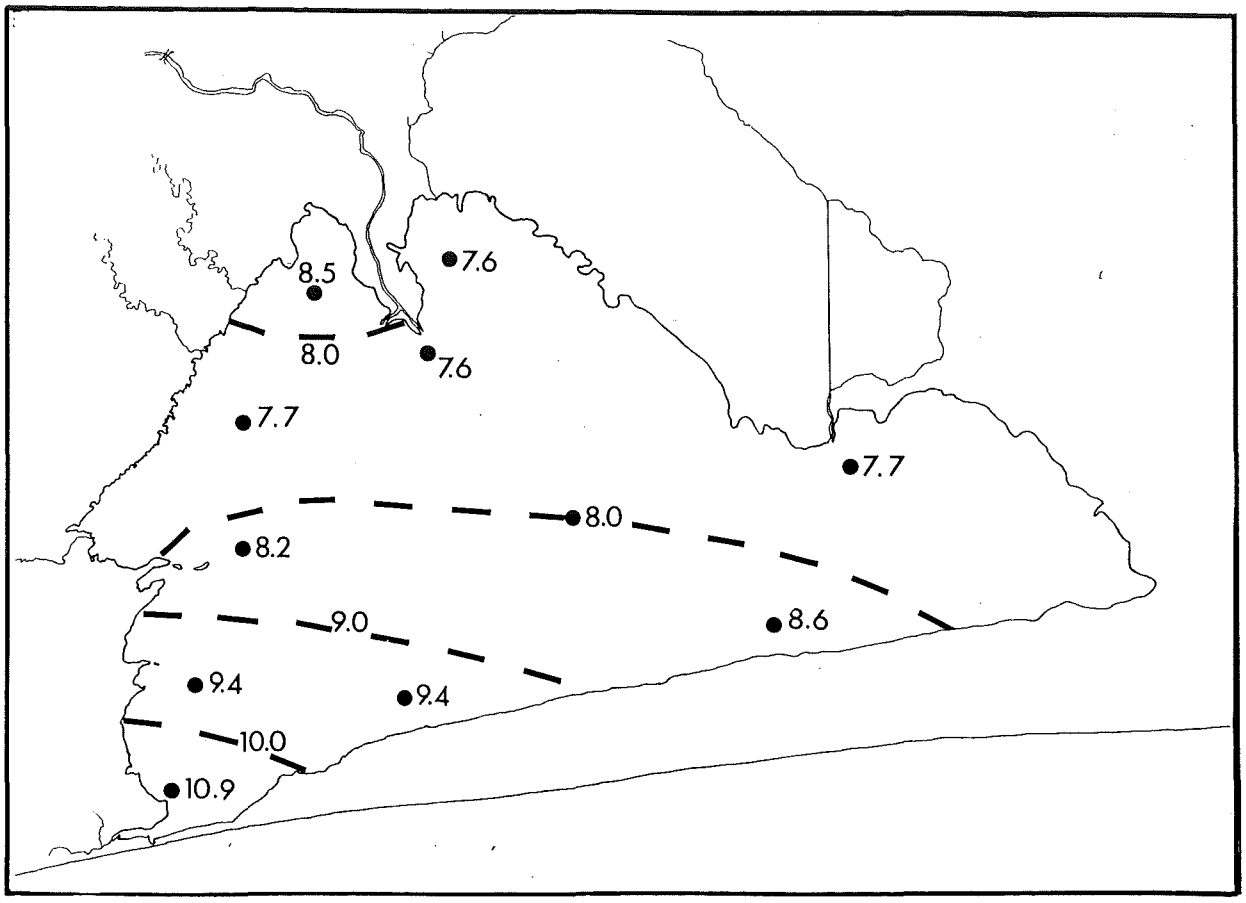

Figure 4/4: Lake Ellesmere: Mean Salinity, 1978-1980. (‰)

the Selwyn, although there were isolated backwaters within the area. It is possible that the eastern end of the lake (Kaituna lagoon) would also be a backwater and have a higher salinity, like Site 10.

Salinity and conductivity are related, and as would be expected, showed the same pattern of concentration. Site 13 had the highest levels of conductivity, as well as the major ions, whereas the sites close to the inflows (4,6,8) had lower conductivities and concentrations of ions. Comparing the inflow composition (section 3.1.2) to these sites (Table 4/3), the rapid mixing of river-water with the lakewater was apparent. The mean concentration of calcium in the Selwyn River was relatively constant at 10.4 ± 0.6 $g.m^{-3}$ (Table 3/4); at site 8, just out from the mouth, it was 38.7 ± 5.2 $g.m^{-3}$, while the overall mean for the lake was 56.1 ± 2.1 $g.m^{-3}$. So although there was a general gradient across the lake, from inflow to outflow, the mixing of riverwater with lakewater took place chiefly at the mouth of the river. This was even more apparent with the mean chloride concentrations in the Selwyn River at 27.6 ± 14.9 $g.m^{-3}$ (Table 3/4), whereas at site 8 it was 2841 ± 610 $g.m^{-3}$. The overall lake mean was only 3557 ± 180 $g.m^{-3}$.

This study can be compared with previous records of ionic composition in the lake. The mean levels of calcium, magnesium, bicarbonate and sulphate were lower than those of the 1973-74 survey. All four ionic concentrations were between 63% and 75% of the earlier means, although the previous means fell well within the range of values found in this present study (Table 4/3). The mean values of total hardness and chlorinity were slightly higher than in the 1973-74 survey.

Further records of chlorinity were presented by Hughes et al. (1974). That study showed that high chloride concentrations were found immediately after lake openings, but that it declined when the lake was closed for a long period. The mean chloride concentration for 1969-1972, based on seven samples was similar to the mean in the present study.

The ionic composition of the lake varies at different times. Figure 4/5D shows the mean salinity of the lake for the period for which measurements were made and Figure 4/5C gives the mean conductivity over the whole period. Conductivity declined between July and September

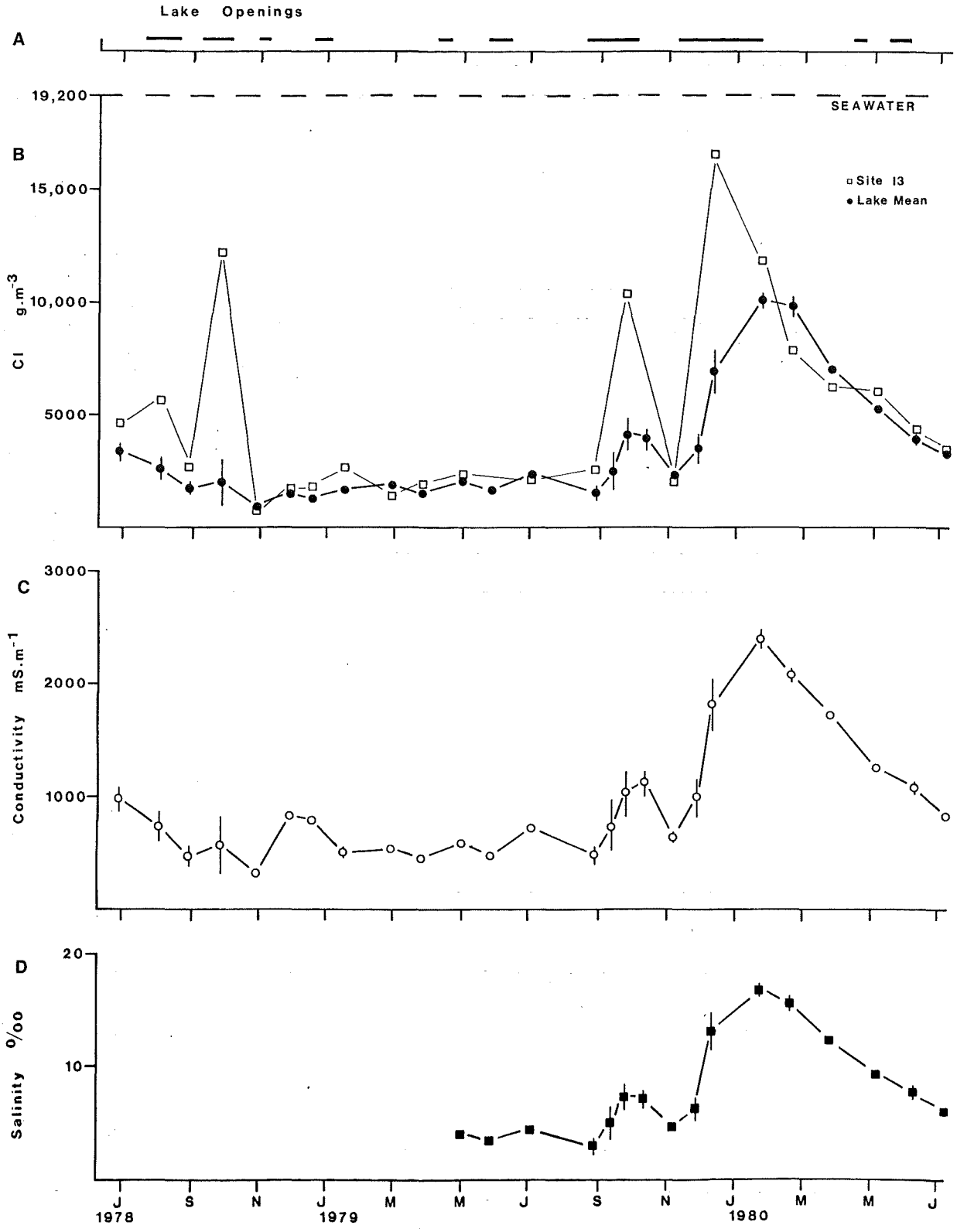

Figure 4/5: A. Lake Openings
B. Lake Chlorinity: Mean (±S.E.), Site 13
C. Mean Conductivity (±S.E.)
D. Mean Salinity (±S.E.)

1978, when a high standard error to the mean at the same time is indicative of a wide variability between sites. In the period November 1978 to late August 1979, conductivity fluctuated slightly but the sites showed less variety. From September 1979 to July 1980 there were two peaks in conductivity, followed in each case by slow declines in the levels. There was a higher standard error as the levels rose than there was as they declined.

Chloride concentration reflects the same trend (Figure 4/5B). The concentrations for Site 13 (nearest the opening) are included on the graph. This site frequently diverged from the mean levels of the lake. In August and September 1978, September and December 1979, there were particularly noticeable variations.

The mean seawater chloride concentration is also shown on Figure 4/5B, and the periods of time the lake was open to the sea in Figure 4/5A. In December 1979, the lakewater at Site 13 had a chloride concentration of 16700 $g.m^{-3}$. This is equivalent to an 88% content of seawater within a localized region of the lake. The mixing of this seawater takes time to occur so that the rest of the lake did not immediately reflect the seawater influx. The peak in the mean concentration for the whole lake was not reached until late January 1980. During February and March 1980, the lake was not open to the sea and the water had time to mix. The chloride concentration of Site 13 fell below the mean of the lake at this time. The lake was again opened in April and by early May the chloride concentration at Site 13 exceeded the mean for the lake again.

Over the period November 1978 to late August 1979, the lake was opened several times, but no opening was long enough to allow much seawater to flow in. For most of this period, the chloride concentration at Site 13 was close to the overall mean concentration. The relative stability of this mean over such a long period probably is a result of an equilibrium between seawater percolation through the shingle spit, evaporation during the summer, and freshwater inflow. Even when no seawater entered the lake directly through an opening the ionic composition remained brackish because of this equilibrium.

4.2.2 Ionic Balance

Table 4/6 gives a mean ionic balance for the lake based on 151 samples taken over one year (Collections 1-14,26). This shorter

Table 4/6: Mean Ionic Balance for Lake Ellesmere.

Cations		Anions	
	$meq.l^{-1}$		$meq.l^{-1}$
Calcium	2.74	Carbonate	0.11
Magnesium	10.63	Bicarbonate	1.12
Sodium	45.66	Chloride	53.47
Potassium	1.69	Sulphate	5.94
	60.72		60.64

Total ionic concentration = 121.36 $meq.l^{-1}$

Total cations - Total anions = 0.08 $meq.l^{-1}$

period does not include the period of high seawater influx. In this table each ion is expressed as a milli-equivalence, and it is noteworthy that the dominant cation is sodium and the dominant anion is chloride. The other ions are in the following order of diminishing importance:

cations: $Na^{+} > Mg^{++} > Ca^{++} > K^{+}$

anions: $Cl^{-} > SO_4^{=} > HCO_3^{-} > CO_3^{=}$

This dominance reflects the influence of seawater within the lake, and confirms the comments by Stout (1975) who emphasized the influence of oceanic salts in coastal lakes of Canterbury.

4.2.3 Plant Nutrients

The plant nutrients are often referred to as minor elements, but this belies their importance within the ecosystem (Golterman, 1975a). This group of essential nutrients includes nitrogen, phosphorus and silica, each of which is required in smaller quantities than the major ions. These nutrients each has its own complex cyclic system and the following discussion will outline this to the extent that it is applicable to an understanding of Lake Ellesmere.

4.2.3.1 Nitrogen

The generalized nitrogen cycle within a lake system has been described by Golterman (1975a), and this provides a basis for discussion. Other reviews are given by Brezonik (1972), Kenney (1973) and Moss (1980).

Inorganic nitrogen occurs predominantly as molecular nitrogen, nitrate, nitrite and ammoniacal nitrogen. The first of these, atmospheric molecular nitrogen (N_2) is a source of nitrogen for phytoplankton through nitrogen fixation by heterocystic blue-green algae. N_2 dissolves in water and establishes an equilibrium with the atmosphere (Golterman, 1975a).

The latter three forms, nitrate, nitrite and ammoniacal nitrogen form an oxidation-reduction series and are used as nutrients by most phytoplankton (Golterman, 1975a), although there is some debate as to the preferential uptake of ammonia compared to nitrate (Brezonik, 1972). Utilization of nitrite by phytoplankton has recently been demonstrated by Latorella et al. (1981). Nitrate is the more stable

dissolved form of inorganic nitrogen and is usually found in high concentrations in freshwater.

Apart from inorganic nitrogen, there is a large pool of nitrogen within organic matter. The organic nitrogen analyzed in this study (see Table 2/7) is largely within the phytoplankton (Chem. Div., DSIR, pers. comm.). The breakdown products in the form of dissolved organic nitrogen are potentially available as a nitrogen source (Moss, 1980). The importance of zooplankton excretion in recycling nitrogen and the role of bacteria are not well understood (McCarthy, 1980). The turnover time of the nitrogen cycle may be 10 - 40 times per year (Golterman, 1975a). Both inorganic and organic nitrogen would be important within the lake ecosystem, if this is the case.

In this survey, no measure has been made of dissolved molecular nitrogen. However, heterocystic blue-green algae have been found in Lake Ellesmere (see Chapter 5), and this is evidence that nitrogen-fixation may be taking place.

The mean concentrations of the nitrogen forms are given in Table 4/3. Nitrate was the most abundant inorganic form, and had an overall mean of 0.639 $g.m^{-3}$, although it ranged up to 3.75 $g.m^{-3}$. The mean concentration of ammoniacal nitrogen was 0.013 $g.m^{-3}$ with a range up to 0.160 $g.m^{-3}$ and the contribution from nitrite is minimal, ranging up to 0.048 $g.m^{-3}$. The organic nitrogen pool was considerable, with a mean concentration of 0.954 $g.m^{-3}$, and a range up to 4.15 $g.m^{-3}$.

The mean concentrations of these nutrients can be compared with those found in 1973-74. Nitrate showed a dramatic increase of 4.26 times its mean level. Nitrite and ammoniacal nitrogen were little changed. Total organic nitrogen, on the other hand, had a mean concentration of less than one half its 1973-74 level.

The spatial distribution of mean concentrations of organic and inorganic nitrogen forms are shown in Figure 4/7. The most evident pattern is the dispersion of the inorganic nitrogen concentration. Sites near inflows, the Selwyn and LII had high mean inorganic nitrogen, especially nitrate levels, but the levels decreased away from these sources. Site 4, close to the Halswell mouth had a rather lower nitrate concentration, and sites on the southern side had means around 0.4-0.5 $g.m^{-3}$. This implies the rivers must be the major sources of nitrate. The mass-flow analysis (section 3.1.2.2.1) confirmed that the

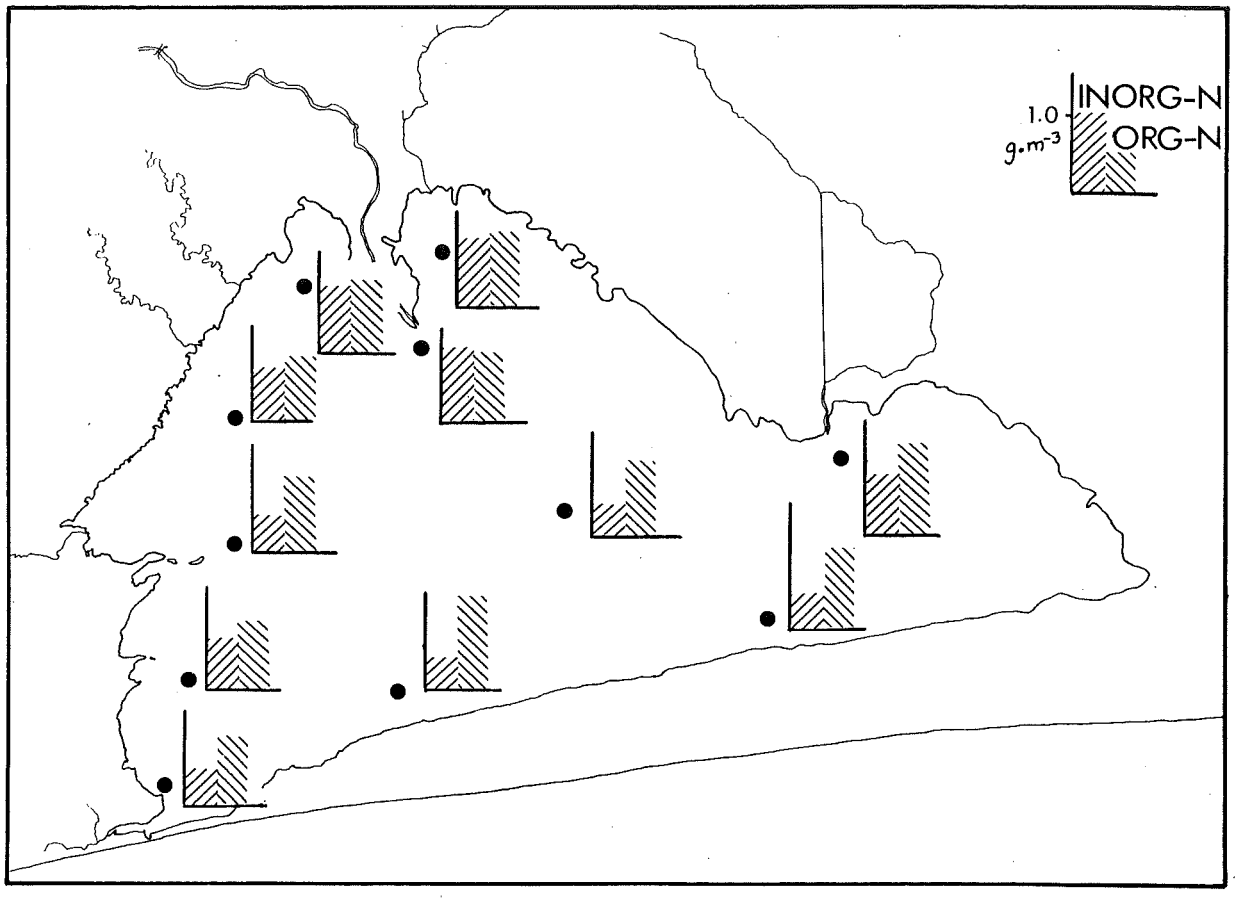

Figure 4/7: Lake Ellesmere: Mean Inorganic and Organic Nitrogen, 1978-1980.

input of nitrogen per unit time was greatest from the Selwyn, with slightly less from the LII, and lower levels from Hart's Creek and the Halswell.

There was no particular pattern in the mean nitrite levels within the lake, but it must be borne in mind that nitrite is a transitional oxidation state within the nitrogen cycle. Ammoniacal nitrogen was most concentrated out from the LII, with other high levels out from the Halswell and Selwyn. Again this must be due to the input of ammoniacal nitrogen from the river inflows. Other levels of ammonia throughout the lake did not show any particular spatial pattern.

Organic nitrogen mean concentrations fell within the range 0.85 - 1.14 $g.m^{-3}$. The highest levels were found out from the Halswell and along the Spit margin but there were no significant variations among the other sites (see Figure 4/7).

The dynamics of the nitrogen cycle are somewhat complex. Figure 4/8A shows how mean inorganic nitrogen levels vary over time. This figure is based on the mean of all sites for each given collection. It shows an annual cycle, with high winter levels and lower summer levels. The winter peaks occurred in August-September and there was a decline during October and November. During the summer of 1979-80 inorganic nitrogen levels were very low, with a mean of less than 0.03 $g.m^{-3}$ over a three month period.

The cycle of inorganic nitorgen is primarily by a conversion to organic nitrogen. Figure 4/8B shows the mean total organic nitrogen over the same period. The increase in the level of organic nitrogen came after the inorganic nitrogen peak. In January 1979 a mean of over 2.0 $g.m^{-3}$ occurred. In the summer of 1979-80 another increase in organic nitrogen occurred, again following the winter nitrate peak. A sharp decline was apparent in 20 days during November 1979, associated with the opening of the lake to the sea (compare Figure 4/5A). On most occasions when the lake was opened, there was an associated sharp decline in the organic nitrogen level. This was particularly noticeable at the end of September and December 1978; May, September and November 1979. It is unclear how at such times seawater influx and freshwater dilution interact to influence the decline of organism numbers, but the decline in organic nitrogen in December 1978 is surely due to a rainfall dilution, since the lake

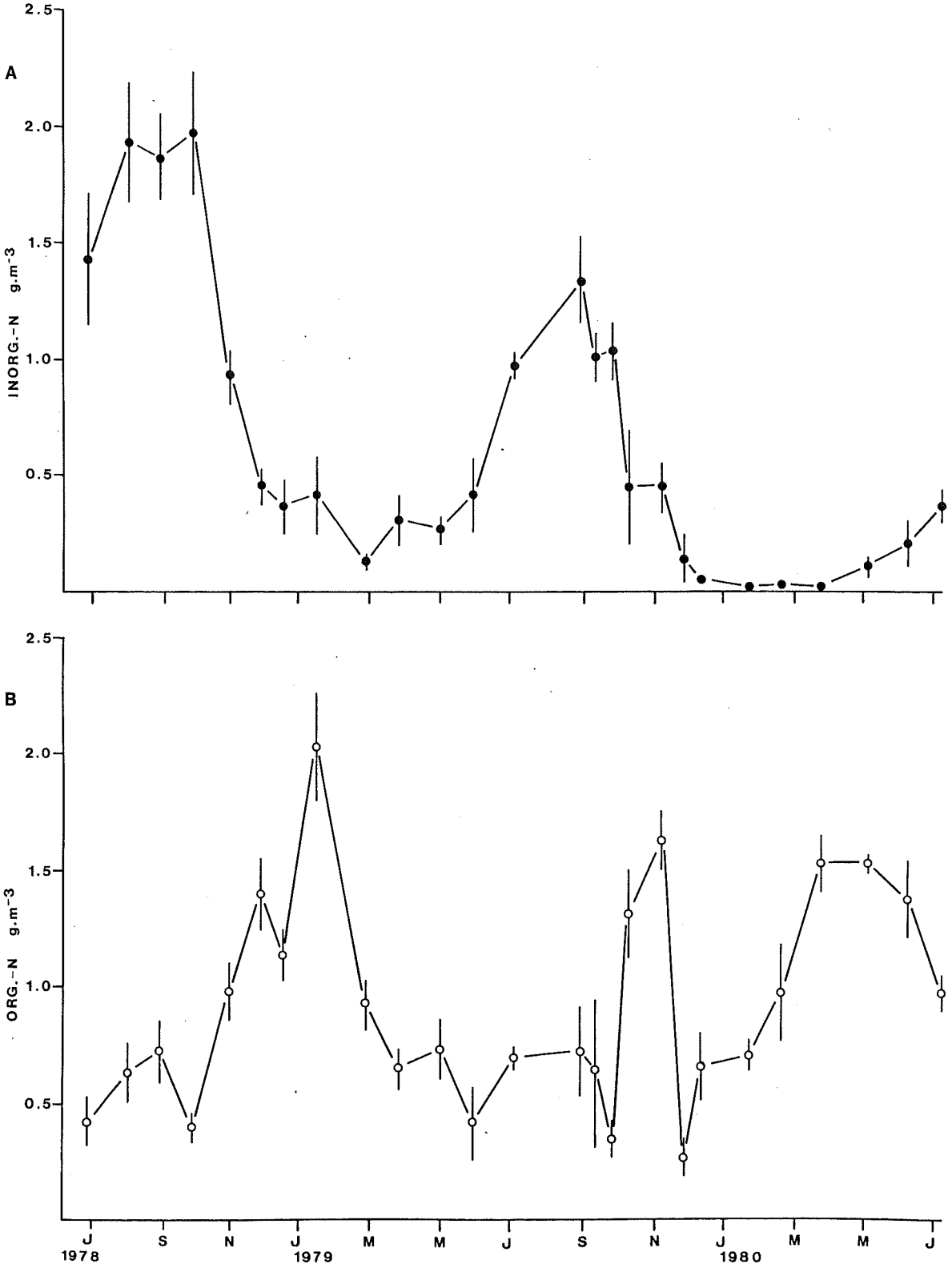

Figure 4/8: A. Mean Lake Inorganic Nitrogen (±S.E.)
B. Mean Lake Organic Nitrogen (±S.E.)

was first opened the day that the decline was noted. At other times the lake had been opened for some time prior to sampling.

The nitrate influx into the lake is relatively constant via the inflows (section 3.1.2.2.1) but it is sometime before the nutrients are mixed throughout the lake. Nitrate levels rise during the winter but decline during the summer, when it is converted to organic nitrogen. This system is modified by the diluting effect of the freshwater input by the inflows and possibly by rainfall. At times of high inflow and/or rainfall, although the nitrogen mass-flow remains relatively constant, its concentration is diluted. This leads to higher lake water levels and the possibility of a lake opening. The opening of the lake (see section 3.2) results in a flushing out of nutrients and organic nitrogen, and a lowering of the lake level.

The nitrogen cycle will be discussed further (section 4.2.7) when the interaction with phosphorus and nutrient loadings are considered.

4.2.3.2 Phosphorus

Phosphorus is an important plant nutrient and its role in eutrophication has been much discussed. The resulting literature is voluminous and often contradictory (Reynolds, 1978). Reviews and symposia, which include consideration of phosphorus, are found in Vollenweider (1971), Rohlich (ed., 1969), Jenkins (ed., 1972), Likens (ed., 1972), Lund (1973), Jenkins and Ives (1973), Golterman (ed., 1977), and Jones and Lee (1982).

The phosphorus cycle within lakes has been discussed at length by Golterman (1975a) but important aspects are detailed by Kramer et al. (1972), Lean (1973) and Ahlgren (1977). The schematic presentation by Golterman (1975a:90) shows that there are essentially two parts to the cycle: the short duration metabolic cycle, and the longer term geochemical cycle, which involves sedimentation processes.

The forms of phosphorus analysed in the present study are soluble phosphorus, and total phosphorus. Soluble phosphorus is the phosphorus immediately available for phytoplankton use and is thought to include more than just inorganic orthophosphate (PO_4-P) (Chemistry Division, D.S.I.R., pers. comm.). Total phosphorus is the sum total of all phosphorus within an unfiltered water sample, including that bound to sediment, and within organisms.

Table 4/3 gives the mean concentrations of soluble and total phosphorus for the two-year sampling period. The overall mean soluble phosphorus for all sites was 0.010 ± 0.002 $g.m^{-3}$, with a range from < 0.001 to 0.086 $g.m^{-3}$. Total phosphorus had an overall mean of 0.151 ± 0.008 $g.m^{-3}$, and ranged from 0.013 to 0.960 $g.m^{-3}$. These mean concentrations were comparable to the mean concentrations found in the 1973-74 survey (Table 4/3).

Figure 4/9 shows the spatial distribution of the site means for total phosphorus. The greatest levels were in the middle of the lake, away from the inflows.

The fluctuation of soluble phosphorus over time is shown in Figure 4/10A. Soluble phosphorus had low mean concentrations for most of the two-year period, except for the period of September - November 1978, when the mean concentration rose to 0.041 $g.m^{-3}$. This rise followed the increase in soluble phosphorus at the inflows (see Figure 3/6B). The only other period when the mean concentration of soluble phosphorus in the lake rose above 0.010 $g.m^{-3}$ was in January 1980, which was also a time of high phosphorus levels in the inflows (Figure 3/6B).

Total phosphorus fluctuations over time are shown in Figure 4/10B. The greatest mean concentrations occurred during the winter of 1979, when the peak of 0.697 $g.m^{-3}$ occurred. This peak was about twice the other high mean concentrations and followed a period of high total phosphorus inflow (see Figure 3/6A). The total phosphorus fluctuations were affected by the suspension of solids within the water column (see section 4.2.6.2).

A comparison of the fluctuations of soluble and total phosphorus does not show evidence of a close relationship (Figs 4/10 A and B). However, a rise in total phosphorus after the peaks in the soluble phosphorus may be noted for some periods. This observation holds for the periods November 1978, April-May 1979, January-February 1980 and May-June 1980. It is not possible to elaborate on this observation since the total phosphorus measurement is of both organismic and sedimentary material. As will be shown in a latter section on nutrient limitation (section 6.5) both processes occurred at different times. Another factor was the short turnover period of the phosphate cycle. Monthly sampling was not likely to show specific transitions between the two forms of

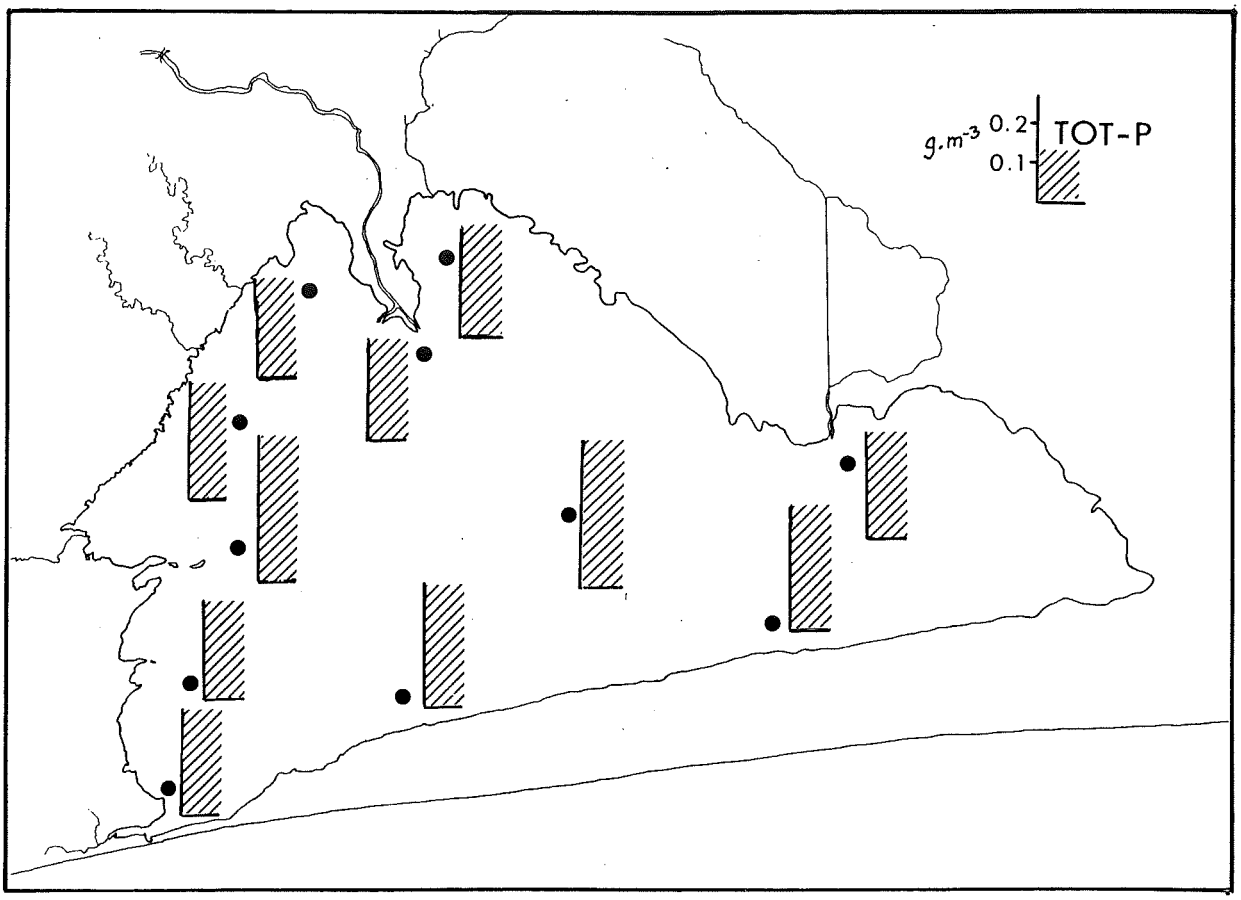

Figure 4/9: Lake Ellesmere: Mean Total Phosphorus, 1978-1980.

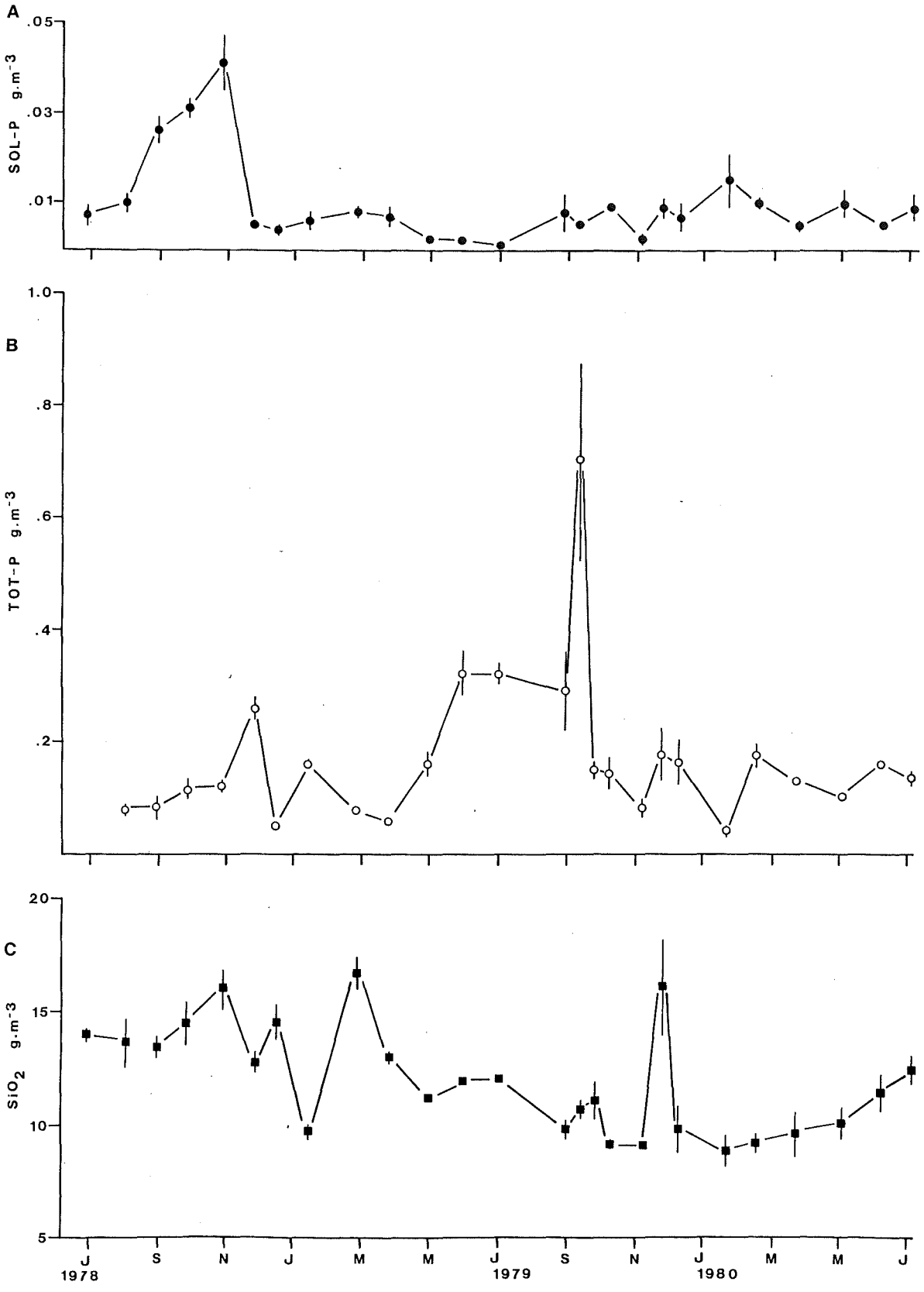

Figure 4/10: A. Mean Lake Soluble Phosphorus (±S.E.)
B. Mean Lake Total Phosphorus (±S.E.)
C. Mean Lake Silica (±S.E.)

phosphorus. The concentrations of both soluble and total phosphorus certainly responded to increases within the inflow waters. This did not give rise to such a marked gradient across the lake as did the concentrations of inorganic nitrogen, but those sites near inflows showed slightly higher soluble phosphorus levels.

4.2.3.3 Silica

Silica is of biological importance in lakewater because diatoms require it for their cell walls (Golterman, 1975a). Up to 15% of the wet weight of diatoms is silica dioxide (Nriagu, 1978).

The mean silica concentration in the lake was found to be 11.9 $g.m^{-3}$, with a range from 1.3 to 22 $g.m^{-3}$ (Table 4/3). This overall mean concentration was lower than for the 1973-74 survey period, and lower than the mean concentration of the contributing inflows (Table 3/4).

There was no apparent difference between the sites throughout the lake, and the means for each site were within the range 10.4 to 12.9 $g.m^{-3}$. However, the lowest levels of silica were found close to the outflow, no doubt due to the diluting effect of seawater. Site 13 had the lowest concentration (1.3 $g.m^{-3}$) in collection 20; and levels of 6.0, 5.5 and 6.1 $g.m^{-3}$ were recorded for the same site in collections 4, 16 and 21 respectively. These were all taken during periods of seawater influx (section 4.2.1).

The mean concentration for the whole lake did not reflect the pattern of seawater influx, except for the period December 1979 to July 1980 (Figure 4/10C). This was a period after a massive influx of seawater, when the mean chlorinity of the lake was affected markedly (see Figure 4/5B). The fluctuations of silica also showed high levels in November, followed by a decrease towards January in both years. There were other periods of fluctuations which were less easily explained, and neither was there any apparent relationship with the inflow levels over time (Figure 3/3C). The peak level of silica in November 1979 coincided with a high level of suspended solid content within the water. This suggests that the silica level may be influenced by that fraction bound within the sediments.

Analysis of silica within the sediments of the lake is beyond the scope of this present study, but it has been shown by studies of

Laurentian Great Lakes that silica levels increase within the deeper sediments of those lakes (Nriagu, 1978). One may hypothesize that as more sediment is resuspended from the lake bottom, silica becomes more evident in the water column.

Although its cycle within Lake Ellesmere is still largely unknown, silica would seem to be in abundant supply. Further analysis of silica in terms of input loading is given in section 4.2.7, and the question of silica limitation is discussed in section 6.5.

4.2.4 Trace Elements

The available data on trace elements in Lake Ellesmere is very limited. It is only possible to note the records of such data without detailed discussion.

Table 4/3 gives records of several trace elements within filtered water samples. Cadmium, copper, manganese and zinc were at the lowest detectable levels on the one collection date when they were sampled. Iron levels were recorded for two collection dates. Strontium, lithium, rubidium and fluoride were analysed on one collection date each.

Table 4/11 provides the available data for the analysis of trace elements within suspended material. Little can be deduced from these results, because of the wide disparity in the minimum detectable level in the two different sets of data presented.

4.2.5 Dissolved Gases and pH

The two dissolved gases to be discussed are carbon dioxide and oxygen. A third gas of importance, atmospheric nitrogen (N_2), has already been mentioned in relation to the nitrogen cycle (4.2.3.1). Both carbon dioxide and oxygen are important because of the role they play in primary and secondary production. Carbon dioxide is closely related to pH, and these two will be discussed together.

4.2.5.1 Dissolved Oxygen

Dissolved oxygen is derived from two main sources: dissolved atmospheric oxygen, and oxygen resulting from primary production. The solubility of oxygen within water is affected by the water temperature and atmospheric pressure (Golterman et al., 1978), but since atmospheric pressure is reasonably constant, temperature is the key factor.

Table 4/11: Trace elements in Suspended Material ($mg.g^{-1}$).

Sites *1	1	2	4	5	6	8
Cadmium *2	2	2	2	<2	<2	2
*3	<100	<100	<100	<100	<100	<100
Copper *2	70	30	6	100	<2	<2
*3	125	1500	<100	<100	100	<100
Iron(%) *2	6.0	7.8	6.7	8.6	9.8	5.3
*3	5.0	4.5	3.8	3.6	4.4	5.1
Manganese *2	40	30	30	25	15	40
*3	3800	4100	3300	5700	3900	2800
Zinc *2	100	150	70	180	10	35
*3	190	160	140	<50	350	320

Sites *1	10	11	12	13	14
Cadmium *2	2	2	2	-	2
*3	<100	<100	<100	<100	<100
Copper *2	<2	<2	10	-	<2
*3	140	<100	<100	<100	<100
Iron(%) *2	8.8	8.9	9.1	-	9.8
*3	4.8	5.3	5.0	5.7	5.0
Manganese *2	30	30	35	-	50
*3	4300	3500	2600	3500	4300
Zinc *2	40	10	25	-	25
*3	250	210	160	280	150

*1 for site location refer Table 2/1.

*2 26 June 1978

*3 27 November 1978

Photosynthesis and respiration may lead to temporary departures from the equilibrium between dissolved and atmospheric oxygen when there is little gas exchange at the water surface (Moss, 1980).

Supersaturation with oxygen can be due to high photosynthetic oxygen production when surface gas exchange is poor, and lower oxygen levels result when respiration uses more oxygen than photosynthesis can produce. It may alternatively be caused by oxygen poor waters from lower levels being mixed with surface waters (Moss, 1980).

The mean concentrations of dissolved oxygen are given in Table 4/3. The mean oxygen concentration was 11.2 $g.m^{-3}$, with a range of 8.7 to 14.3 $g.m^{-3}$. The means for the individual sites varied little within the range 10.83 to 11.69 $g.m^{-3}$. Figure 4/12A gives the mean oxygen concentrations for the period during which data was collected. Given the biological requirements of plants and aquatic animals, oxygen shortages are unlikely to have been a problem during the study period. The small standard error bars associated with each mean also implies a uniformity throughout the lake at any one time. The periods when the dissolved oxygen level was low were periods characterized by high total suspended sediment content within the water (see section 4.2.6.2 and Figure 4/14A). This suspended sediment content is the total inorganic and organic sediment, and is thought to have the effect of limiting light penetration. Moreover wind which mixes the water and stirs up the sediment also mixes the water in lower reaches which is potentially low in oxygen content.

The water sometimes was supersaturated with oxygen (Figure 4/12A). Such a period occurred from August 1979 to May 1980 (with exceptions in September, November and February), and would seem to be due to phytoplankton production of oxygen at times of high biomass levels (see section 6.3). During the winter (May - August 1979 and June-July 1980), the saturation of oxygen was much lower, and it is significant that in winter phytoplankton populations were lower. The three exceptional periods, September and late November 1979, and February 1980 (Collections 15, 19 and 22, respectively), when the oxygen content was less than the equilibrium concentration, were during an active growing period. This implies that primary production must have been limited at these times. On

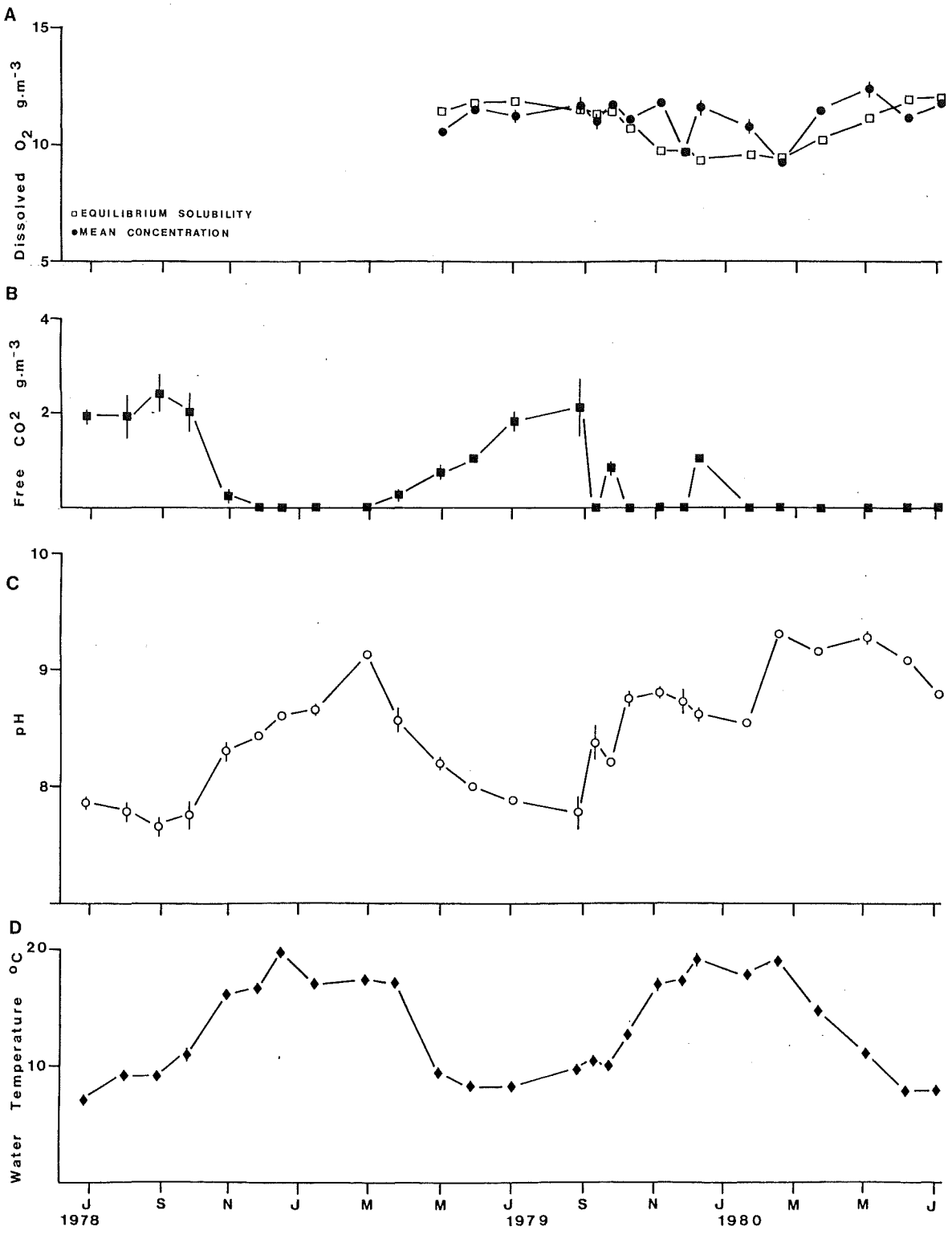

Figure 4/12: A. Dissolved Oxygen: Equilibrium solubility and Mean Concentration (±S.E.)
B. Mean Free Carbon Dioxide (±S.E.)
C. Mean Lake pH (±S.E.)
D. Water Temperature at Time of Sampling

two of these occasions the suspended sediment content of the water was in excess of 100 $g.m^{-3}$, and light penetration was potentially a limitation on primary production. The lower production of oxygen may therefore be interpreted as a self-shading effect caused by the phytoplankton population. The importance of wind should not be neglected in this respect (see section 4.2.6.2).

4.2.4.2 Carbon dioxide and pH

Carbon dioxide within water is regulated by a series of equilibria within the calcium bicarbonate system (Golterman, 1975a). The equilibria are influenced by pH, so that at pH greater than 8.3 no free carbon dioxide is present.

The mean concentrations for carbon dioxide and pH levels are given in Table 4/3. The overall mean carbon dioxide concentration was 0.684 $g.m^{-3}$, which reflected the overall mean pH of 8.45. The range of values was of greater importance, because phytoplankton are affected by extreme conditions. The overall range of pH was 7.2 - 9.5, and for carbon dioxide from zero to 11 $g.m^{-3}$.

Figure 4/12B gives the mean carbon dioxide concentrations over the two year period. On several occasions the carbon dioxide level was low, especially during the summer periods when pH rose above 8.3. Figure 4/12C gives pH changes over time. A seasonal cycle is evident. pH levels were low in winter but rose during spring to a peak in the late summer.

During the latter part of 1979, there were distinct variations from the general pattern. This was probably due to the seawater influx during this period (section 4.2.1). The pH of seawater is 8.0 (Bates, 1975), and during September 1979 the influx caused an increase in the overall lake pH. The influx in December 1979 entered the lake when the pH was high and consequently it reduced the overall pH level. The lake gradually became mixed, the salinity fell and the lake pH then returned to the previously observed pattern.

Just as the pH was influenced by seawater influx, so it was influenced by the freshwater inflows. The river inflows have more stable pH levels (section 3.1.2.6.1), and this constant input was reflected in the site means (Table 4/3). The sites closest to the inflows, sites 4,6 and 8, had mean pH values lower than other sites within the lake.

The complexity of the bicarbonate system within the lake as reflected by pH also affects the phytoplankton by influencing population successions through species limitation. This aspect will be discussed in a later chapter (Chapter 6).

4.2.6 Other Features of Biological Importance

Apart from the water chemistry there are other features of the lake which have direct bearing upon the phytoplankton ecology. These features include water temperature and water transparency. The first of these features is closely related to the climate of the region (see 3.3), and the second is associated with the amount of suspended solid content within the water.

4.2.6.1 Water Temperature

Water temperature has been recognised as a factor affecting phytoplankton growth (Moss, 1973b). The optimum temperature at which growth occurred was 21.4°C for a group of eutrophic plankters, with little growth occurring below 4°C or above 35°C.

Water temperature as reported in this section is the temperature of the water just below the surface at the time of collecting each sample. This does not give the full diurnal range of temperature, but continuous temperature records were not available to determine the full range of temperature during the study period.

Figure 4/12D shows the mean water temperatures over the two year period. As expected, this follows the seasonal pattern of air temperature (section 3.3.2). The range of temperature was 6.5 to 21.5°C, with an overall mean of 13.5°C. The low standard error indicates the general uniformity of temperature throughout the lake on any one collection day.

Although temperature profiles were not attempted, the shallow nature of the lake suggests that it is probably not thermally stratified, except perhaps for short periods associated with the few calm days.

4.2.6.2 Water Transparency

Water transparency for light penetration is a necessary condition for photosynthesis by the phytoplankton (Moss, 1980). Light

reflection and scattering can therefore limit the photosynthetic process. The depth at which photosynthetically active radiation (P.A.R.) drops to 1% of the surface intensity is the compensation point (Talling, 1971). This is the point at which photosynthesis is equal to respiration. Above this level is the euphotic zone (Moss, 1980), in which there is sufficient light to allow photosynthesis.

The depth of the euphotic zone was calculated from the surface light and the extinction coefficient of light within the water column. The intensity of surface light can be reduced by surface reflection at certain angles, and the extinction coefficient depends on dissolved pigments and sediment content, which include chlorophyll related and non-chlorophyll organics and inorganics (Verduin, 1982). Talling (1960) has shown that phytoplankton can cause self-shading at high population levels (compare 4.2.5.1). These levels of high sediment content will be related to total phytoplankton biovolume (Chapter 6).

The light measurements used in this study were based on photosynthetically active radiation, from which the light extinction coefficient has been calculated after Moss (1980):

$$\varepsilon = \frac{1}{Z}\ 2.303\ (\log_{10} I_0 - \log_{10} I).$$

I_0, is the surface intensity; I, intensity at depth.

Z, was either one meter or one-half meters, according to the depth of the lake at the time (see Chapter 2.2).
From this calculation the euphotic depth (Z_{eu}) has been calculated:

$$Z_{eu} = \frac{4.6}{\varepsilon}$$

(Moss, 1980)

Table 4/13 shows the overall mean for all suspended solids as 88.5 $g.m^{-3}$. However, the range of values was unusually wide, from 1 to 889 $g.m^{-3}$. Figure 4/14A shows the solid content in the water column over the two year period. For most of the time it was less than 100 $g.m^{-3}$ but the content could reach very much higher levels.

Table 4/13: Total suspended solids and light measurements.

	Units	Mean	S.E.	Min.	Max.	n.
Total Suspended Solids	$g.m^{-3}$	88.5	6.8	1	889	253
Surface light	$\mu E.m^{2}.s^{-1}$	942	36	147	2211	202
Light extinction coeff (ε)	ln units m^{-1}	5.87	0.16	1.54	15.37	202
Euphotic depth (Zeu)	m	0.94	0.05	0.29	2.97	202

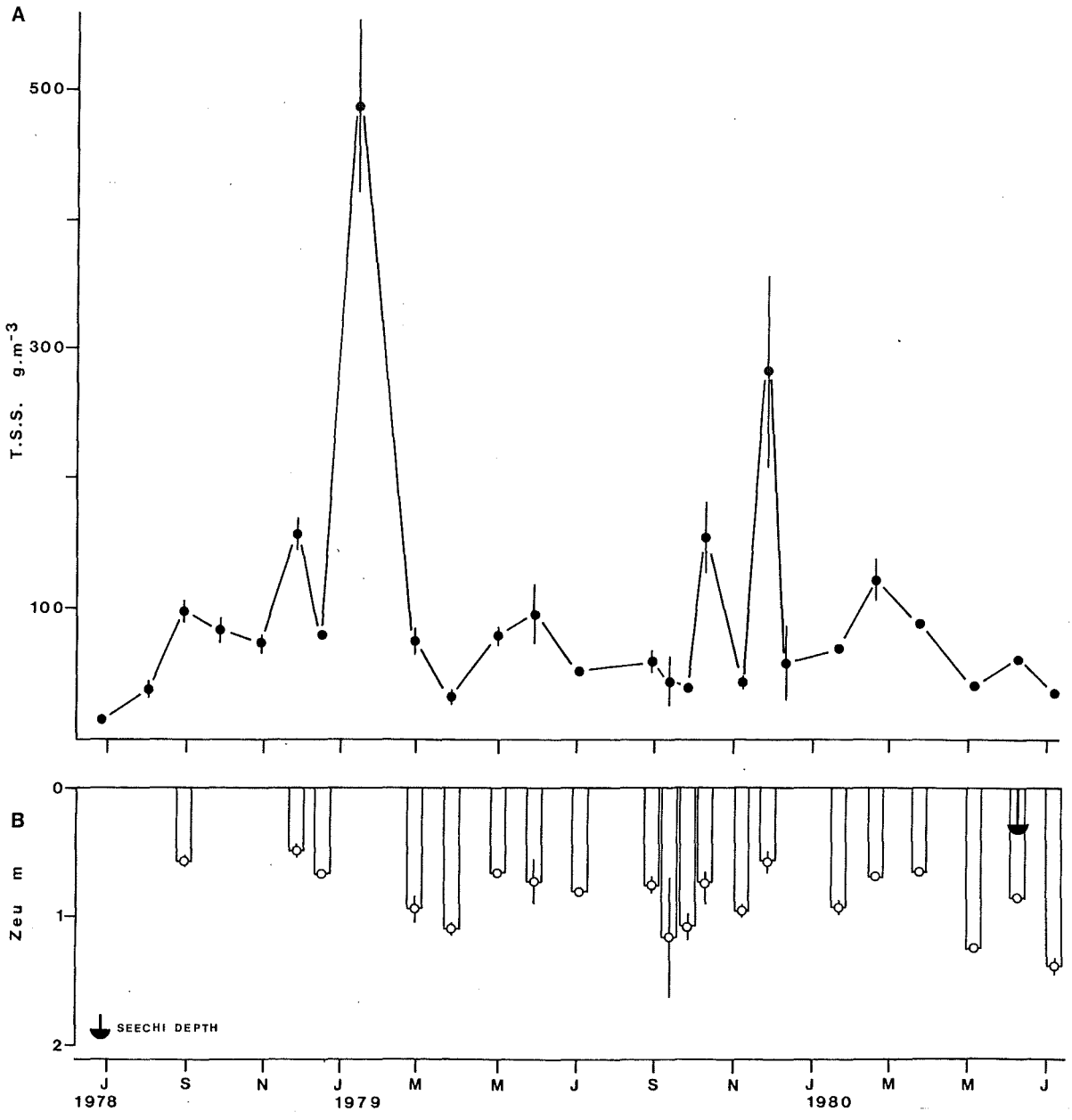

Figure 4/14: A. Mean Total Suspended Solids (±S.E.)
B. Mean Euphotic Depth (±S.E.) and Seechi Disk Depth.

Wind is plainly one factor and there is a relationship between wind data (see Figure 3/12, and section 3.3.3) and sediment levels. Most of the high sediment levels (especially that of November 1978) can be related to the higher than average daily wind-run.

The photosynthetically active radiation (P.A.R.) at the surface of the lake should reflect the seasonality of the temperate zone. However, there are flaws in this data and they must be used with caution. The light was only recorded on reasonably calm days, which were often clearer and brighter than the average. On occasions when the surface was rough, no accurate light readings were possible. The recorded mean, however, was 942 $\mu E.m^{-2}.s^{-1}$, with a range from 147 to 2211$\mu E.m^{-2}.s^{-1}$, taken over 202 samples (Table 4/13). The minimum value occurred on a day of 100% cloud cover, in March 1979.

The light extinction coefficient (ε) ranged from 1.54 to 15.37 ln units m^{-1}. The mean coefficient was 5.87. The mean depth of the euphotic zone (Z_{eu}) calculated from the above values was 0.94 m, and ranged from 0.29 to 2.97 (Table 4/13). When the depth of the lake is borne in mind (see section 4.1.2) it seems unlikely that light penetrates to the whole of the bottom of the lake on many occasions.

Figure 4/14B shows the mean depth of the euphotic zone over the two year period, which shows an inverse relationship to the graph of total suspended solids. Although some records are missing, the evidence suggests that the euphotic zone is reduced when there is a high level of sediment in the water column. The most noteworthy case was in December 1979, which coincided with the influx of seawater (see section 4.2.1). On this occasion the deepest euphotic zone (2.97m) was found close to the opening in a region of high salinity. The very shallow euphotic zones (or high extinction coefficients) were toward the middle of the lake. Possibly the influx of seawater pushed the sediment back to a high concentration in the centre of the lake. A distinct line of demarcation was observed between the two water types at this time and the seawater was easily distinguished from the green coloured lakewater.

It is apparent that usually little light reaches the bottom of the lake, and consequently lower regions of the water column are not conducive to photosynthesis. There is reason to subject light to examination as a limiting factor in a later section (section 6.5).

4.2.7 Chemical Loadings and Budgets

Water chemistry involves more than the study of chemicals within the lake water column. It is necessary to analyse the nutrient loading of the lake and relate it to the trophic status of the water. Recent research notably by Vollenweider (1971; 1975; 1976 a,b) and Vollenweider and Dillon (1974) has aimed to analyse the annual supply and loss of nutrients per unit area or volume. Golterman and Kouwe (1980) have summarized this work.

For a simple flow-through lake system, which is vertically and horizontally mixed, the potential total concentration can be calculated from parameters such as the input loading, residence time, lake volume, mean lake depth and sedimentation rate. Golterman and Kouwe (1980) suggest two methods to calculate total concentration: one calculated from conservative elements such as sulphate and chloride; and a second taking sedimentation of non-conservative forms, such as plant nutrients into account. Sedimentation can be due to chemical processes (carbonate and phosphorus) or due to biological activity (nitrogen, phosphorus and silica).

Reckhow (1981) reviewed the requirements for nutrient budget modelling and emphasized the care needed in analysing lake data. Examples of nutrient budgets for individual lakes are found in Dillon (1975) and Vollenweider (1976b) for phosphorus; Hetling and Sykes (1973) for nitrogen and phosphate; and Gibson (1981) for silica.

The available data for Lake Ellesmere does not allow a complete budget to be given for any of the nutrients. The lack of water residence time data due to the irregular openings of the lake (see section 3.2), and the lack of information on sedimentation rates both cause problems in calculation. There are also uncertainties associated with the changing depth, surface area and the contribution of groundwater and rainfall. Other lakes described in the literature cited had permanent inflows and outflows and relatively constant volume. Lake Ellesmere on the other hand has been shown to be very variable in several of these aspects.

The input loadings for nitrogen, phosphorus and silica are given in Table 4/15. This is based on the mass-flow data calculated earlier (section 3.1.2.2) and includes assumptions associated with area and depth. The loadings do not take into account input from

Table 4/15: Nutrient loadings from inflows.

	Nitrate	Tot-N.	Sol.-P	Tot-P	Silica
Total Mass-Flow $g.s^{-1}$ *1	51.620	57.761	0.327	1.652	230.1
Areal loading $g.m^{-2}.yr^{-1}$ *2	8.957	10.022	0.057	0.287	39.92
Volumetric loading $g.m^{-3}.yr^{-1}$ *1	2.898	3.243	0.0184	0.093	12.92

*1 Table 3/5

*2 Areal loading based on area at 0.99 m contour; Table 4/1

*3 Volumetric loading based on mean depth at 0.99 m contour; Table 4/2

rainfall or other sources such as drains and groundwater. The areal loadings are:

total nitrogen	10.022 $g.m^{-2}.yr^{-1}$	(89% nitrate nitrogen)
total phosphorus	0.287 $g.m^{-2}.yr^{-1}$	(20% soluble phosphorus)
silica	39.92 $g.m^{-2}.yr^{-1}$	

When expressed on a volumetric basis, which includes further approximations in terms of depth, the loadings are:

total nitrogen	3.243 $g.m^{-3}.yr^{-1}$
total phosphorus	0.093 $g.m^{-3}.yr^{-1}$
silica	12.92 $g.m^{-3}.yr^{-1}$

Vollenweider (1971) gives the "permissible" and "dangerous" loadings for lakes at various depths. These categories represent the levels beyond which eutrophication could be expected to be accelerated. Taking Vollenweider's shallowest mean depth (up to 5 m), both the total nitrogen and total phosphorus are greater than the "dangerous loading" level. The nitrogen loading is more than five times greater, and the phosphorus loading twice as great.

Work subsequent to Vollenweider's has proposed other models for critical loadings of phosphorus, including variables such as relative residence time (Vollenweider, 1976a), or flushing rate and retention rate (Dillon, 1974).

The complexity of the Lake Ellesmere system, due to irregular openings suggests that this analysis be accepted with caution, until such time as fuller appraisal of the irregular flushing can be made. In view of the long agricultural margin to Lake Ellesmere and the considerable hydrological input from rainfall (section 3.1.1), these loadings calculations are probably too low.

4.2.8 Trophic status

The strict definition of the trophic status of a water body was given previously in relationship to the nutrient content of the water (see section 1.1). In this context the inorganic forms of the plant nutrients, nitrogen and phosphorus are of particular importance (Moss 1980).

The studies best known on the subject of the limits of different trophic states are Sawyer (1947) and Vollenweider (1971). Sawyer surveyed several Wisconsin lakes and concluded that 'nuisance' algal growths could be expected when inorganic nitrogen and phosphorus at spring overturn exceeded 0.30 $g.m^{-3}$ and 0.01 $g.m^{-3}$ respectively. Vollenweider in a detailed discussion of Thomas's survey of 47 Swiss alpine lakes gave guidelines regarding nutrient concentrations for various trophic states. He noticed that these concentrations correspond to levels at the time of winter overturn, prior to substantial increases in standing crop in spring.

A comparison of the present data for Lake Ellesmere with the work by Vollenweider (1971) provides a basis for a positive statement on the trophic status of the lake. However it should be emphasized that the situation of Lake Ellesmere on the edge of a lowland plain is somewhat different from any high alpine lake in a continental region. It will be argued at a later stage (section 6.5) that the growth of algae is not potentially limited by the low temperature in the winter period in Lake Ellesmere. Ice does not form on this lake and stratification is not known to occur (see section 4.2.6.1). As a consequence the concept of a winter overturn may be misleading. It was shown earlier (section 4.2.3.1) that the occurrence of inorganic nitrogen was cyclic, with levels high in winter and lower in summer, whereas phosphorus showed no such pattern (section 4.2.3.2).

Vollenweider (1971:43) defined polytrophic as the highest trophic state, beyond eutrophic. In Ellesmere, the winter peaks of inorganic nitrogen were in September 1978 and August 1979, at 1.973 $g.m^{-3}$ and 1.339 $g.m^{-3}$ respectively (Figure 4/8A). A comparison of these values with Vollenweider's study (1971) puts Lake Ellesmere on the border of or within the polytrophic category with regard to nitrogen. Even the overall mean concentration of inorganic nitrogen over the whole two year period at 0.656 $g.m^{-3}$ (Table 4/3, sum of nitrate, nitrite and ammoniacal nitrogen) is well within the minimum range for a eutrophic state.

The overall phosphorus peak was in September 1979 at 0.697 $g.m^{-3}$ (Figure 4/10B). This level is well within the polytrophic minimum of 0.100 $g.m^{-3}$ set by Vollenweider. The overall mean concentration for total phosphorus in Lake Ellesmere over the two year period was 0.151 $g.m^{-3}$, which is still well above the eu-polytrophic level.

In the light of both the inorganic nitrogen and the phosphorus parameters, it can be noted with some degree of certainty that Lake Ellesmere is in a highly eutrophic to polytrophic state. Even conclusions based on the mean concentrations rather than the winter maximum levels are not substantially different.

Another comparison can be made with the nitrogen and phosphorus levels given by Sawyer (1947). It was suggested that 'nuisance' algal blooms were more likely to appear when inorganic nitrogen was above 0.3 $g.m^{-3}$ and phosphorus was above 0.01 $g.m^{-3}$ at spring overturn. The concentrations in Lake Ellesmere are above these levels for both the winter maxima and the mean concentrations by several times. Consequently it is little wonder that Lake Ellesmere exhibits frequent algal blooms (see section 6.3).

4.3 FACTOR ANALYSIS OF PHYSICO-CHEMICAL VARIABLES

Throughout the previous discussion, the complexity of the physico-chemical environment has been emphasized. This has been due in part to the inter-relationships between variables (e.g. temperature and dissolved oxygen) and also to the difficulties of measuring underlying variation (e.g. chlorinity, conductivity and salinity). This present section will explore some of these related measures and attempt to show the underlying variation by way of factor analysis.

Table 4/16 shows a correlation matrix for the whole range of water chemistry and climate variables (as defined in Tables 2/4, 2/5, 2/7). This is based on Spearman's rho (Conover, 1980) as calculated by the NONPAR CORR Subprogram (SPSS, 1975). Significant correlations at the 0.05 and 0.001 levels are shown. The high incidence of correlation between several variables makes factor analysis a useful technique for extracting the underlying patterns.

Principal component analysis is probably the best known method of factor analysis. Detailed descriptions of the method are found in Seal (1964) and Rummel (1970). Jeffers (1978) gives an example comparable to the persent analysis.

Factor analysis as described by SPSS (1975) has three stages: the preparation of the correlation matrix, the extraction of initial factors and the rotation of the terminal factors. The correlation matrix

Table 4/16: Level of Significance of Spearman Correlation Coefficients for Physico-Chemical Variables.

	NO_3-N	NO_2-N	NH_4-N	T.O.N.	SOL.-P	TOT.-P	SILICA	TOT.S.S	PH	CONDUCT	HARD	CALCIUM	MAG	SODIUM	POTASS	CARB	CO_2	CL	SO_4	BICARB	DOXY	TEMP	SALINITY	SURFLI	CLOUD	WINDRUN	WINDFOR	RAIN	SUNSHINE
NO_3-N																													
NO_2-N	*																												
NH_4-N		+																											
T.O.N.	*		*																										
SOL-P			+																										
TOT-P	+				*																								
SILICA	*	*	+	*	*																								
TOT.S.S.	*	*		*	+	*																							
PH	*	*	+	*		+	*	+																					
CONDUCT.	*	*	*		+		*	+	*																				
HARD	*	*	*		+		*	+	*	*																			
CALCIUM	*		*		*		+	*	+	*	*																		
MAG	+		*	+	*		*	*		*	*	*																	
SODIUM	+		*	*	*		*	*		*	*	*	*																
POTASS	*		+	+	*		*	*		*	*	*	*	*															
CARB	*	*	+	*		+	*	+	*	*	*																		
CO_2	*	*		*		*	*	+	*	*	*					*													
CL	*	*	*		+		*	+	*	*	*	*	*	*	*	*	*													
SO_4		+	*	+	*		*	+		*	*	*	*	*	*	*		*												
BICARB	+		*	*	*		+			*	*	*	*	*	*	*	+	*	*											
DOXY	+	+						*	*	+	*			+				+	+	*										
TEMP	*	*		*	+	*	+	*	*			*	*	*	*	*	*		*		+									
SALINITY	*	*			*	*	*	+	*	*	*	*	*	*	*	*	*	*	*		+	*								
SURFLI	*	*						*	*			+	*	+	+	*	*		*	+		*								
CLOUD			*	*		+			*							*			+	*	*	*								
WINDRUN	*	*						*	+			*	*	*	*		*		*	+	+	*	*	*	*					
WINDFOR	+		*				+	*	+	*	*	+	*	*	+	+		*	*		+	*		+		*				
RAIN	*	+	*		*	*	*			*	*	*	*	*	*		+	*	*	*	+					*				
SUNSHINE	*	*		*			*	*	*				+	+	*	*	*		+		+	*	*	*	+	+	+	*		

α
< 0.05 +
< 0.001 *

used for the factor analysis is that generated by Pearson's product-moment correlation. Although this correlation coefficient has an assumed underlying normal distribution when used as an inferential statistic, no assumptions are involved if used descriptively (Rummel, 1970). The present study is a descriptive analysis and therefore there is no necessity to check each variable for normality, or to use the rank order (Spearman) correlation.

Principal components analysis was undertaken using the FACTOR subprogram of the SPSS (1975) package. An iteration technique was used and the final solution was rotated so as to maximize the variance of each column (TYPE = PA2, ROTATE = VARIMAX).

Because of correlations and of some cases with missing data, only a selection of variables were analysed. This selection included:

plant nutrients:

nitrate, nitrite, ammoniacal nitrogen, soluble phosphorus, total phosphorus, silica;

expression of water composition:

total hardness, conductivity, pH;

water transparency measures:

total suspended solids, euphotic depth;

climatic variables:

temperature, cloud cover, sunshine hours, windrun and rainfall.

The data set chosen for analysis was that for which phytoplankton counts were made with the intention that the solution might be related ecologically to the community dynamics (Chapter 6). Thus the data set was restricted to 206 cases. In the few cases with missing data, the missing variable was estimated by taking a mean value from the results for that collecting trip.

Table 4/17 summarizes the components extracted from this data set. It includes seven factors, the first five of which cover over 88.4% of the total variation within the data. The first eigenvalue was 3.69, which makes up 32.9% of the variability, and the second 20.5%. The eigenvalues for factors 6 and 7 were still comparatively large, which probably means that no one or two underlying factors alone account for the variability of the data. It was not possible to apply a test of significance to the solution because this would

Table 4/17: Eigenvalues of the factors extracted from the physico-chemical data.

Factor	Eigenvalue	Percent Variability	Cumulative Percentage
1	3.69	32.9	32.9
2	2.30	20.5	53.4
3	1.91	17.1	70.4
4	1.11	10.0	80.4
5	0.90	8.0	88.4
6	0.72	6.3	94.9
7	0.57	5.1	100.0

require an unjustified assumption that there was a multivariate normal distribution (see earlier; and Jeffers, 1978). Jeffers (1978) suggested that eigenvalues of less than 0.8 were unlikely to have any practical value ecologically. Therefore only the first five factors are likely to be of ecological importance.

The coefficients of the functions defining the factors, after rotation are given in Table 4/18. The coefficients greater than ± 0.40 are indicated for ease of interpretation. The first factor was essentially related to climate, with temperature, cloud cover, sunshine and windrun all loaded heavily on it. The second factor had total hardness and conductivity loaded on it and can be interpreted as expressing ionic composition of the water. Nitrate and soluble phosphorus were positively loaded and oppositely loaded with pH, on the third factor. This factor was therefore related to plant nutrients, if the high pH is related to nitrogen depletion (see section 6.5). Factor 4 had more nutrient variables (ammoniacal nitrogen and silica) positively loaded, but cloud has a moderately negative loading. In the case of the fifth factor, only rainfall had a positive loading. Although not shown in Table 4/18, total phosphorus, total suspended solids and euphotic depth were all highly loaded on factor 6. This factor therefore expressed the degree of light penetration into the lake and explained only 6.5% of the variability. Nitrite was most highly loaded on factor 7 with a coefficient of only 0.34.

These factors will be considered again in Chapter 6 when they will be correlated with species data. At this stage it may be concluded that the variability and complexity within the environment can be reduced to five main factors. Two factors (1 and 5) were related to climate; two (3 and 4) were related to nutrient status, and one (factor 2) was related to the ionic composition of the water.

Table 4/18: Eigenvectors of the first five orthogonal factors, after varimax rotation.

	Coefficients for factors				
	1	2	3	4	5
Nitrate-N	-0.18	-0.26	0.83*	0.12	-0.03
Nitrite-N	-0.15	-0.17	0.15	0.03	-0.02
Ammonia-N	0.08	-0.14	0.04	0.52*	0.11
Soluble - P	<-0.01	0.25	0.38*	0.28	0.19
Total - P	-0.10	-0.21	0.12	-0.20	-0.28
Total Hardness	0.10	0.91*	-0.21	-0.20	-0.08
Silica	-0.03	-0.29	0.02	0.82*	-0.02
Suspended Solids	0.22	0.10	0.02	0.15	-0.01
pH	0.09	0.32	-0.83*	0.13	0.04
Conductivity	0.10	0.88*	-0.19	-0.26	-0.08
Temperature	0.77*	0.24	-0.29	0.10	0.33
Cloud Cover	0.42*	-0.09	0.36	-0.41	0.07
Sunshine	0.84*	0.06	-0.18	0.03	-0.29
Windrun	0.87*	0.03	0.03	<-0.01	-0.09
Rain	-0.10	-0.14	0.02	0.08	0.86*
Euphotic Depth	-0.08	0.07	0.09	< 0.01	0.05

*indicates the highest loading of a variable on any factor.

CHAPTER 5

PHYTOPLANKTON FLORA

5.1 INTRODUCTION

Until 1974 only partial studies had been made of the phytoplankton of Lake Ellesmere and only on diatoms (Crosby and Wood, 1959; Wood et al, 1959; Wood, 1961). In the review of the lake (Hughes et al., 1974) Flint listed 39 taxa from six algal divisions, emphasising that the flora was characteristic of eutrophic water and largely dominated by chlorococcalean and blue-green algae.

Many of the taxa previously reported have been observed again in the present research, but several species were recorded for the first time. Due to the ecological importance of the Chlorophyta and Cyanophyta within the lake a detailed description is given of the species indentified from these groups. It has also proved necessary to give a detailed synonymy for several families and genera in this taxonomic section because of confusion that has arisen when comparing the species present with those recorded elsewhere in New Zealand. An endeavour has been made to use the most acceptable taxonomic name according to the International Code of Botanical Nomenclature (1978), with reference to recent revisions of various groups. For example, the genus Ankistrodesmus has been divided into two genera which renders previous New Zealand determinations unsatisfactory.

It has not been possible to identify all the rarer species of phytoplankton. Some Chrysophyceae were found in preserved samples and could not be directly compared with live material because of changes of body shape induced by preservation. Most diatoms occurred at such low densities (see Chapter 6), that cleaning for identification was impossible (Hasle and Fryxell, 1970), and attempts to culture diatoms for identification were largely unsuccessful (see Chapter 2).

The taxonomic arrangement of this chapter is based on Fott (1971) with modifications as in Christensen (1980). The composition of the flora will be briefly discussed and compared to standard indices of trophic status.

5.2 CYANOPHYTA

In the past, taxonomic treatments of the blue-green algae have been based largely on cell morphology and colony forms (Fritsch, 1945; Fott, 1971; Bold and Wynne, 1978), and at the specific level this led to the differentiation of species on the basis of morphological features such as cell size. More recently, culture work and study of herbarium sheets have suggested that some morphological variation is due to environmental influences. This premise necessitated significant revisions in the blue-green algae taxonomy, undertaken by Drouet and Daily (1952; 1956) and Drouet (1968; 1973; 1977). These revisions have resulted in vast reductions in the numbers of species of blue-green algae, and the compilation of extensive synonymies. This approach has been subject to some criticism and is not widely used at present (Komárek, 1958; Bourrelly, 1970; Fott, 1971; Bold and Wynne, 1978).

This present study will follow a more classical approach, as found in Fott (1971), and wherever possible the appropriate synonym will be included.

Division: Cyanophyta

Unicellular or multicellular, prokaryotic algae, with chlorophyll a, phycobiliproteins and carotenoids. Reproduction by division, endospores, exospores or hormogonia. Two orders represented:

Order: Chroococcales

Single celled or colonial forms, lacking endospores and exospores. Reproduction by binary fission or by fragmentation.

Order: Oscillatoriales (Hormogonales)

Filamentous trichomes, lacking endospores and expospores. Reproduction by hormogonia, or akinete formation. Heterocysts present in some families.

Order: Chroococcales

The order Chroococcales includes the unicellular and non-coenobial colonial forms, which do not produce endospores or exospores (Bold and Wynne, 1978). Only two genera are included in the present treatment, both belonging to the family Chroococcaceae. Two other genera previously recorded by Flint (in Hughes et al., 1974),

Gomphosphaeria lacustris Chodat and Coelosphaerium keutzingianum Nägeli (inadvertently listed amongst the Chlorococcales (Flint, in Hughes et al. 1974:26)), have not been rediscovered in the present study. The two genera recorded for the Chroococcaceae are: Microcystis and Merismopedia.

Genus: Microcystis Lemmermann[1]

Microcystis has been the subject of much discussion because of the circumscription of the generic characters. At the beginning of the century, the genus included plants with small globose cells densely aggregated in structureless mucilage (West and Fritsch, 1927). Geitler (1925; 1932) expanded this to include plants with elongate cells, and recognised 23 species. Elenkin (1938, not seen; cited by Desikachary, 1959) extended Microcystis to include Aphanocapsa, but transferred species with ovoid or cylindrical cells to Aphanothece. Drouet and Daily (1939) reduced Microcystis to 3 species of phytoplanktonic algae, but suggested several others deserved inquiry. Other species, previously referred to Microcystis, were transferred to Aphanocapsa and Aphanothece depending on whether their cells were spherical or elongate. More recently, Drouet and Daily (1956), in revision of all the coccoid blue-green algae, recognised the genera Anacystis and Coccochloris[2] for the species with spherical,

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[1] Microcystis Lemmermann conserved against Microcystis Kützing (see International Code of Botanical Nomenclature, 1978).

[2] Anacystis and Coccochloris as used by Drouet and Daily are both inadmissible as generic names. Aphanothece Nägeli has been conserved, with the type species A. microscopica Nägeli, against Coccochloris C. Sprengel, with type C. stagnina Sprengel (International Code of Botanical Nomenclature, 1978).

Drouet and Daily (1956) listed Aphanothece microscopica as a synonym for Coccochloris stagnina, and therefore Coccochloris sensu Drouet et Daily is invalid, and must revert to the conserved name Aphanothece Nägeli. Drouet and Daily (1957) defended their action in that the genus was considerably enlarged in conceptual limits.

Likewise, Microcystis Lemmermann has been conserved against Microcystis Kützing and other synonyms (International Code of Botanical Nomenclature, 1978). The conserved type species is Microloa aeruginosa Kützing.

Drouet and Daily (1956) have included Microcystis as a synonym for Anacystis sensu Drouet and Daily, and have included the conserved type, Microloa aeruginosa as a synonym to Anacystis cynea Dr. et Daily. This is not acceptable, since the case for conservation was made and accepted. Therefore, Microcystis should be used in preference to Anacystis, unless both genera are accepted.

and ovoid to cylindrical cells, respectively. They distributed the species of Microcystis, by synonymy, between the eleven species of these two genera.

Komárek (1958) strongly criticised Drouet and Daily with regard to Aphanothece clathrata, and this criticism can be extended, because they looked at exsiccatae material and often dismissed material without reference to the descriptions and illustrations of the authors. Komárek "would prefer the type to be considered as the description and illustration, rather than dried material, especially when the species had already been confirmed many times" (1958, p.29, translation).

Komárek (1958) recognised Diplocystis as synonymous with Microcystis and included species with both spherical and ovoid cells. In Czechoslovakia, 5 planktonic species were recognised; several were questionable specimens and numerous synonyms were used. Microcystis Lemmermann sensu Komárek has since been conserved against the synonym Diplocystis Trevis (International Code of Botanical Nomenclature, 1978).

Desikachary (1959) also recognised the independent genus Microcystis, and included 18 species for the Indian region. Fott (1971) suggested there may be about 25 species in the genus.

Five species of Microcystis have been recorded in New Zealand (Chapman et al., 1957; Sarma and Chapman, 1975; Cassie 1979). One species is included within this present study.

Microcystis minutissima W. West 1912: 41

(Geitler, 1925: 63; 1932: 145).

Colonies irregularly shaped 40-140 µm. or larger, with hyaline mucilage. Cells ellipsoidal, spherical after cell division, 0.8-1 µm. in diameter (rarely 1-2 µm), 1.1-1.5 µm in length (rarely to 2 µm), bluegreen in colour.

Microcystis minutissima was first described from marshes on Clare Island, Ireland and was subsequently included in European floras (Geitler, 1925, 1932). It was characterised by the small cell sizes, and also by the ellipsoidal cell shape. Microcystis minutissima was therefore closely related to Aphanothece, in that the cells were not spherical but ellipsoidal, and at cell division they were not hemispherical. However, it was planktonic (West, 1912), which distinguishes it from species of Aphanothece (Geitler, 1932). Elenkin (1938, not seen; cited by Drouet and Daily, 1956) transferred this species to Aphanothece as

A. saxicola f. minutissima in making a distinction between Aphanothece with oblong to cylindrical cells, and Microcystis with spherical cells. Nygaard (1949) suggested a relationship of M. minutissima with Aphanothece clathrata var. brevis. Komárek (1958) considered this an unjustified variety because the length of the cells varied during the vegetative phase in the same population.

However, Komárek (1958) included M. minutissima among a list of questionable species, for which no material had been seen by him or otherwise incompletely described. Drouet and Daily (1956) listed Microcystis minutissima West as a synonym for Anacystis incerta Dr. et Daily.

The material from Lake Ellesmere is planktonic, forming irregular colonies (Fig. 5/1 A). The cells are ellipsoidal, 0.9 - 1.5 µm. wide, 1.8-2.8 µm. long, and without a pseudovacuole. Colonial mucilage is hyaline and homogenous. This species was in Lake Ellesmere in the winter 1979, and dominant in the flora during the summer and autumn of 1980.

The cell sizes recorded are so much larger than those given by Geitler (1925, 1932) that some doubt concerning the determination may be felt. However, no other description is appropriate. Other species of Microcystis with elongate cells include the bryozoan epiphyte, M. orissica West, and M. elabens Kütz. var. minor Nygaard with longer cells (Geitler, 1932). Desikachary (1959) included M. litoralis (Hansg.) Forti as a salt water species. Although the cells were ellipsoidal, they were much wider, being 3-5 µm. wide. Among Aphanothece, the species closest to the present material were A. nidulans Richter but cells were up to 3.5 µm. long; and A saxicola Näg. with wider and longer cells (Desikachary, 1959).

Microcystis minutissima West is the most appropriate name for the present material, and as such is a new record for Lake Ellesmere and New Zealand.

Genus: Merismopedia Meyen

Merisomopedia is easily distinguished from other Chroococcaceae by the form of the colony. Cell division occurs in 2 perpendicular planes, resulting in a regular tabloid colony (Geitler, 1932; Komárek, 1958; Fott, 1971). The cells are globose, oblong before division, subspherical

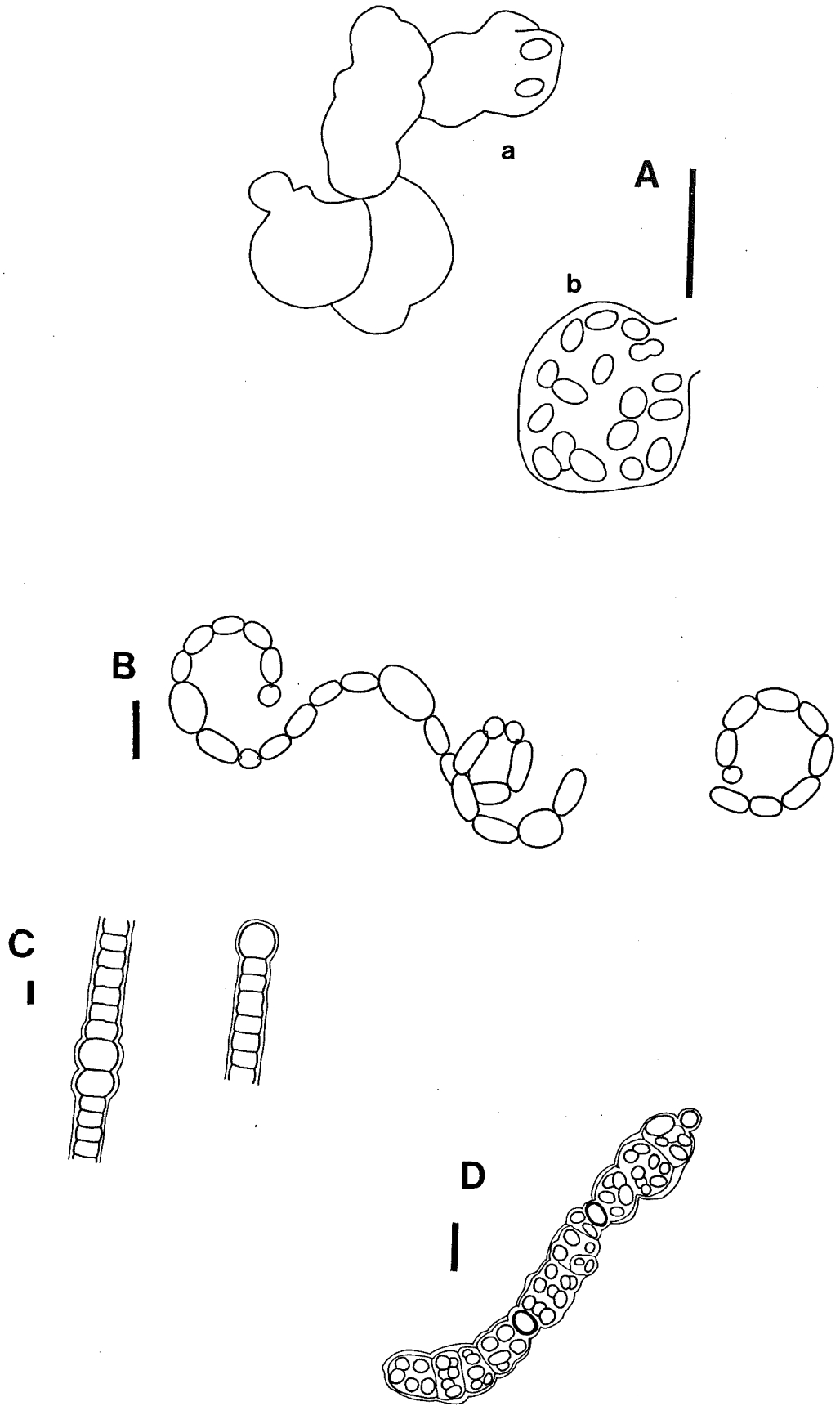

Figure 5/1: Cyanophyta. A. Microcystis minutissima a. colony b. cell arrangement; B. Anabaena sp.; C. Nodularia spumigena b. terminal akinetes; D. Nostoc sp. Scale 10 µm.

after division, and arranged in an homogeneous mucilage in groups of four (Desikachary, 1959). About 13 species, mostly planktonic, have been described from both freshwater and marine environments (Geitler, 1932; Komárek, 1958).

Drouet and Daily (1956) list Merismopedia Kützing as a synonym of Agmenellum Brébisson. They failed to recognise that Meyen used the name Merismopedia in 1839 (the same year that Brébisson described Agmenellum) and Kützing's 1843 use of Merismopedia was not the earliest (Komárek, 1958). Buell (1938) also pointed out that another reference by Meyen in his Pflanzen-Physiologie of 1839 was in fact the first reference to the genus, and not that most frequently cited as in "Wiegmann's Archiv fur Naturgeschichte," for 1839. Komárek (1958) was of the opinion, however, that if there is any question as to priority of Agmenellum over Merismopedia that a case should be made for conservation of Merismopedia Meyen.

From New Zealand, two species have been recorded. Merismopedia glaucum (as Agmenellum quadruplicatum) (Chapman et al. 1957) and Merismopedia elegans (Sarma and Chapman, 1975). For Lake Ellesmere, two species are now recorded.

Merismopedia tenuissima Lemmermann 1898c: 154

(Geitler, 1932:263; Komárek, 1958:43; Desikachary, 1959:154)

Cells, pale-blue green, closely packed in colonies of 16-100 cells. Shape of cells is spherical or subspherical, 1.3 to 2 µm. in diameter.

This species is widespread in freshwater and brackish water, and often planktonic (Komárek, 1958). It is distinguished by the cell sizes, and lack of gas vacuoles. The material from Lake Ellesmere fits well with this description, with cells in the mid-range, at 1.5 µm. diameter. It was present in the plankton in the summers of the study period.

This is a new record for Lake Ellesmere and New Zealand.

Drouet and Daily (1956) give Merismopedia tenuissima Lemm. as a synonym for Agmenellum quadruplicatum Bréb.

Merismopedia punctata Meyen

(Geitler, 1932:263; Desikachary, 1959:155)

Colonies small, 4-64 cells. Cells loose or dense in mucilage, 2.5-3.5 µm. in diameter, spherical to ovoid, pale blue-green.

This species occurs often in standing water amongst other algae, also planktonic, and in thermal waters (Geitler, 1932; Komárek, 1958). There is some overlap in cell sizes with M. glauca, but only at the top of the size range (Geitler, 1932), and M. glauca only appears secondarily in the plankton (Komárek, 1958). Buell (1938) considered M. punctata to be more variable than widely accepted, and gave the range at cell size as 1.2 - 3.9 µm., and reduced M. tenuissima to a synonym, along with some of the vacuolate species. Komárek (1958) considered M. tenuissima, M. glauca, and M. punctata as separate species.

The material from Lake Ellesmere had cell sizes mostly about 3 µm. in diameter, and only rarely larger than 3.5 µm., and was found consistently in the plankton for most of the sample period, but less frequently in winter. Merismopedia punctata is therefore recorded for Lake Ellesmere, along with M. tenuissima. Both were found in the lake at the same time, but the size classes did not overlap, as suggested by Buell. It is maintained here that they are separate species.

This is a new record for Lake Ellesmere and New Zealand, although the genus had previously been noted for the lake (Flint, in Hughes et al. 1974). The Drouet and Daily (1956) synonym for M. punctata Meyen is Agmenellum quadruplicatum Bréb. They have recognised only two species, Agmenellum quadruplicatum and A. thermale for the whole genus.

Order: Oscillatoriales (= Hormogonales)

This order includes the filamentous blue-green algae, which do not produce endospores or exospores. Reproduction is by hormogonium formation, and in some cases akinetes are formed (Bold and Wynne, 1978; Fott, 1971). Further separation into families is based on the presence or absence of heterocysts, and the presence or absence of branching.

Bourrelly (1970) used an alternative classification, with the sub-class Hormogonophycideae (= Hormogonales), separating true branching from non-branching or false branching groups at the ordinal level. Both Bourrelly (1970) and Fott (1971) end up with a similar arrangement of families.

The filamentous blue-green algae do not play an important place in the planktonic flora of Lake Ellesmere. They have not been

directly counted (see Chapter 2), but have been isolated using culture techniques, and recorded in bloom condition. It is necessary to consider these organisms as occasional members of the plankton community, and to record their presence.

The two families represented are Oscillatoriaceae (Oscillatoria, Spirulina) and Nostocaceae (Nostoc, Anabaena, Nodularia).

Family: Oscillatoriaceae.

The Oscillatoriaceae includes the genera with uniserate, cylindrical trichomes, without heterocysts, and without branching.

Two genera are represented in Lake Ellesmere: Spirulina and Oscillatoria. For New Zealand, only one species of Spirulina has previously been recorded, Spirulina calderia Tilden (Kaplan, 1956; as Cyanidium (Tild.) Geitl. see Sarma and Chapman, 1975). Oscillatoria is more numerous, with more than 30 species recorded (Chapman et al. 1967; Flint 1966; Sarma and Chapman, 1975; Cassie and Freeman, 1980).

The starting point for the taxonomy of this family is Gomont (1892) (See International Code of Botanical Nomenclature, 1978).

Genus: Spirulina Turpin ex Gomont 1892: 249

A genus characterized by a helically spiralled trichome (Bold and Wynne, 1978). These spirals may be very close, or distant. Previously this genus was separated from Oscillatoria because of the spiral habit, and from Arthrospira in that there appeared to be a lack of transverse cell walls (Bold and Wynne, 1978). This however is not the case, as shown by electron microscopy (Holmgren et al., 1971). The genus has about 30 species, represented in freshwater, brackish water and marine environments (Geitler, 1932; Fott, 1971).

Bourrelly (1970) incorporated Spirulina as a subgenus of Oscillatoria, whereas Drouet and Daily (1968) recognised the genus, but included only the species S. subsalsa.

Only one species is recorded from the plankton of Lake Ellesmere. Another species, Spirulina subtilissima has recently been recorded, attached to frames within the lake amongst other algae (MacRaild, Botany Department, University of Canterbury, pers. comm.). This species has a narrower trichome, and is more tightly coiled (Desikachary, 1959).

Spirulina major Kützing

(Geitler, 1932:930; Desikachary, 1959:196)

Trichome 1-2 µm. wide, regularly spiralled, blue-green. Spirals 2.5-4 µm. wide, and 2.7-5 µm. distant.

This species is of cosmopolitan occurrence, from fresh and brackish water bodies (Geitler, 1932). Komárek (1958) does not include it amongst the planktonic species for the genus, so it is possibly a transient member of the plankton in Lake Ellesmere.

The material from Lake Ellesmere occurred only in liquid culture from a whole water plankton sample taken at site 11 on February 18, 1980. The trichome width was 1-1.5 µm. and the spirals were 2-2.5 µm. wide and 3-5 µm. distant. This is a new record for Lake Ellesmere and New Zealand.

Genus: Oscillatoria Vaucher ex Gomont 1892:198

This is a large genus with about 100 species (Fott, 1971), or more (Bourrelly, 1970). The trichomes are cylindrical, unbranched, and may, or may not have a delicate sheath (Bold and Wynne, 1978). Typically, the cells are shorter than broad, except for the rounded apical cell.

Many species of Oscillatoria have been recorded for New Zealand (Chapman et al., 1957; Flint, 1966; Sarma and Chapman, 1975; Cassie, 1978; Cassie and Freeman, 1980), although none had previously been found in Lake Ellesmere.

Oscillatoria subtilissima Kützing

(Geitler, 1932: 950: Desikachary, 1959:215)

Trichome single or few together, yellowish green, 1-1.5 µm. broad, straight or curved, septa indistinct, without gas vacuoles. Known from plankton in brackish and freshwater.

Crow (1923) questioned the validity of this species, but retained it because of the very narrow trichome. Komárek (1958), however, does not list O. subtilissima among the planktonic species of the genus.

The material from Lake Ellesmere was determined from an unialgal culture, isolated from a plankton sample collected near site 13.

The trichome width was 1.1-1.3 (-1.5) µm. and the cells were very indistinct. On agar medium the culture was a yellowish to green

colour. This fits the description of O. subtilissima very well, since few other species of Oscillatoria have such narrow trichomes.

Drouet (1968) included Oscillatoria subtilissima Kützing under the synonym for Schizothrix calcicola (Agardh) Gomont, having distinguished between the two genera on whether or not the terminal cell has a thickened outer wall. Drouet included 40 pages of synonyms for Schizothrix calcicola, which incorporated most of the very narrow trichome species from Calothrix, Plectonema, Phormidium and Lyngbya. It is proposed here to recognise Oscillatoria subtilissima as a specific entity, and as such it is a new record for both Lake Ellesmere and New Zealand.

Family: Nostocaceae

The family Nostocaceae includes the genera with uniseriate, non-polar trichomes. The trichomes may be free or in a common mucilage, and heterocysts may be present or absent; if present, intercalary or terminal (Desikachary, 1959; Bourrelly, 1970).

From the family Nostocaceae three genera are now recorded for Lake Ellesmere. They were occasional members of the phytoplankton, isolated by culture technique or recorded in bloom condition only.

Genus: Anabaena Bory ex Bornet et Flahault 1888:224[1]

This genus is similar to Nostoc, except the trichomes are not within a firm gelatinous colony, but occur either singly, clumped or in bundles. The trichome is uniformly broad throughout, with sheath absent or diffluent. Heterocysts are generally intercalary. Akinetes, which are essential for specific determination, are solitary or grouped, adjacent to heterocysts (Desikachary, 1959; Bourrelly, 1970; Fott, 1971).

Many species of Anabaena have been recorded for New Zealand (Chapman et al., 1957; Flint, 1966; Sarma and Chapman, 1975; Cassie

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[1]Bory (1822) used the spelling Anabaina, but since the nomenclature for the heterocystic Nostocaceae began with Bornet and Flahault (1886-1888), the orthography Anabaena must be accepted (International Code of Botanical Nomenclature, 1978). Drouet (1978) and Humm and Wicks (1980) are in error suggesting Anabaina should now be used.

1978; Cassie and Freeman, 1980). For Lake Ellesmere, Anabaena has previously only been recorded to generic level (Flint in Hughes et al., 1974). In this present study, one species has been identified from a preliminary collection off the mouth of the Selwyn River.

Anabaena flos-aquae Brébisson ex Bornet et Flauhault 1888:228
(Geitler, 1932:890; Komárek, 1958:142; Desikachary, 1959:414)

Trichome colonial or single twisted or spirally arranged, without sheath. Cells ellipsoidal, sometimes spherical, barrel-shaped to cylindrical, 2.5-11-12 µm. by (2.5)-3-7-(8?) µm. Heterocysts single, intercalary, spherical, barrel-shaped to ellipsoidal, 4-5(-9) by 5-8.5 µm. Akinetes solitary or up to four side by side, either near the heterocyst or away from it, oval to cylindrical, slightly curved, (13-)15-35-(55) by 5.5-13(-14) µm.

This species is cosmopolitan amongst the plankton of standing waters (Geitler, 1932). It is distinguished from Anabaena spiroides and A. circinalis by its smaller dimensions (Komárek, 1958).

The material from Lake Ellesmere was collected off the Selwyn River mouth in April, 1978 (Fig. 5/1B). It did not appear during the routine sampling programme, although it was isolated using culture techniques. The dimensions of the sample from Lake Ellesmere fit into Komárek's description rather than that of Geitler. The vegetative cells were mostly elongate 5 µm. by 7.5-11 µm., whereas the heterocysts are closer to spherical, 4-5 µm. diameter. The akinetes are also shorter than given by either Geitler or Komárek, at 8 by 9-12 µm. Despite these discrepancies Anabaena flos -aquae is the most appropriate determination.

This is the first record of this species from Lake Ellesmere, although the genus was recorded in 1974 (Flint, in Hughes et al., 1974). Anabaena flos-aquae has been reported for New Zealand on a number of occasions (Chapman et al., 1957; Flint, 1966). It has been suggested that some strains of this species may be toxic and cause "very fast death" of animals, although this has not been reported for New Zealand as yet (Flint, 1966; Cassie, 1979).

Genus: Nostoc Vaucher ex Bornet et Flahault 1888:181

Nostoc is a large genus with about 50 species, often with a large gelatinous colony found most frequently attached to substrate.

Komárek (1958) suggested there were only 2 planktonic species N. kihlmannii and N. planctonicum.

The thallus is mucilaginous, solid or hollow, free or attached. Filaments are flexuous, curved, or entangled. Cells are spherical, barrel-shaped or cylindrical, heterocysts are intercalary, and akinetes are spherical or oblong adjacent to heterocysts (Desikachary, 1959; Bourrelly, 1970).

The material from Lake Ellesmere was isolated from a sample taken near site 13 in April, 1978 (Fig. 5/1D). Because of the lack of akinetes, it was not possible to fully determine this species. However the thallus was tightly coiled, 10-15 µm. wide, and the trichome 3-5 µm. wide. Cells were spherical to ellipsoidal, heterocysts ellipsoidal 8-10 µm. This material is close to Nostoc punctiforme (Kützing) Hariot (see Geitler, 1932, Desikachary, 1959), but has much larger heterocysts.

About 12 species of Nostoc have been recorded for New Zealand (Chapman et al., 1957; Flint, 1966; Sarma and Chapman, 1975).

Genus: Nodularia Mertens ex Bornet et Flahault
1888:243 nom. cons.

Nodularia is a free, filamentous, blue-green algae with a sheath. The trichome in vegetative state is uniform in width, uniseriate with a hyaline sheath. The cells are distinctly shorter than wide, discoid. Heterocysts are intercalary, with akinetes spaced between (Desikachary, 1959; Bourrelly, 1970; Nordin and Stein, 1980).

The genus has recently been revised by Nordin and Stein (1980) to include only two taxa, Nodularia spumigena and N. harveyana. Other taxa are included as synonyms, or excluded.

One species is recorded for Lake Ellesmere.

Nodularia spumigena Mertens ex Bornet et Flahault
emend. Nordin et Stein 1980:1215.

Vegetative cells 7.5-16.0 µm. wide; width to length ratio 2:1-10:1; sometimes with gas vacuoles. Filaments usually with thick, colourless, transparent sheath. Heterocysts subspherical to disc-shaped, wider than long, 8-16 µm. wide, 2-10 µm. long. Akinetes subspherical to disc-shaped, 8-18 µm. wide, 6-15 µm. long, usually in a series, occasionally single or in pairs.

This species occurs in tychoplankton to euplankton of marine, brackish or inland saline environments.

Nodularia spumigena is distinguished from N. harveyana by larger cells, heterocysts and akinetes.

The material from Lake Ellesmere fits well within this species, with cells 9-11 µm. wide, and akinetes to 15 µm. wide (Fig. 5/1C). The trichome was either straight or spiralled. Nodularia occurred occasionally in plankton samples, and was most evident in bloom condition in March, 1981 (see Appendix 2).

Nodularia spumigena has previously been recorded for Lake Ellesmere and other localities in New Zealand (Flint in Hughes et al., 1974; Sarma and Chapman, 1975). It is noted as being toxic to cattle, sheep and dogs (Flint, 1966; Cassie, 1979).

Drouet (1978) recombined Nodularia spumigena as Nostoc spumigena (Mert.) Dr., as one of only two species of Nostoc, among the four species of the Nostocaceae with constricted trichomes.

5.3 CHLOROPHYTA

Several genera of the Chlorophyta have been the subject of recent taxonomic revisions. They also form a large part of the flora, both in terms of known species and community size (see Chapter 6). The present discussion will be limited to the classes and orders represented in the lake. Fott (1971), Bourrelly (1972) and Bold and Wynne (1978) provide general background to the division.

In the arrangement adopted here, in contrast to Fott's arrangement, the small prasinophyte flagellates are removed from the order Volvocales into a separate class, the Prasinophyceae.

5.3.1 Prasinophyceae

The separation of the Prasinophyceae from the other green algae has been suggested by Manton et al. (1963), Pickett-Heaps (1975), Stewart and Mattox (1975), and Moestrup (1978). Round (1971b) suggested that the differences should be recognised at the divisional level. Others, including Fott (1971), and Bold and Wynne (1978) still include the prasinophyte genera within the Volvocales.

Bourrelly (1966) has changed his subdivision in his second edition (1972) and incorporated the Prasinophyceae as a new class. Norris (1980), in his general review, surveys favourably the support for separation of this group. Three genera are now reported for the first time from Lake Ellesmere: Pyramimonas, Nephroselmis and Mantoniella. They are members of two separate orders: Pyramimonadales (Pyramimonas), and Pedinomonadales (Nephroselmis and Mantoniella).

Order: Pyramimonadales

Family: Pyramimonaceae

Pyramimonas sp.

Pyramimonas was identified from live material collected on 29 September, 1980 (Fig. 5/2C). The distinctive appearance of the quadriflagellate, lobed cell was immediately recognised. The cells were 18-20 µm long and 10-11 µm wide. They were slightly tapering towards the posterior, with a bulge in the region of the eyespot. Four flagella emerged from the apical invagination. Within the cell the chloroplast was lobed, with a posterior pyrenoid, which had starch plates on either side of it. An eyespot was associated with the chloroplast, approximately two-thirds of the way down the cell, in one of the lobes of the cell. No electron microscopy was undertaken to show scale form. Therefore no specific determination can be made.

Pyramimonas has about 42 species, from freshwater to marine environments (Maiwald, 1971), and several have been recorded from New Zealand (Taylor, 1974).

Order: Pedinomonadales

Family: Pedinomonadaceae

Two genera from this family have been recorded in this present study: Nephroselmis and Mantoniella.

Nephroselmis sp.

Nephroselmis was identified from live samples collected on 3 September 1980, and also cultured from a sample of 7 July 1980.

The shape of the cell appeared to vary from kidney shape to more obovate (Fig. 5/2B). This is possibly due to the asymmetry of the cell, seen in different views. No thickness was measured. The two

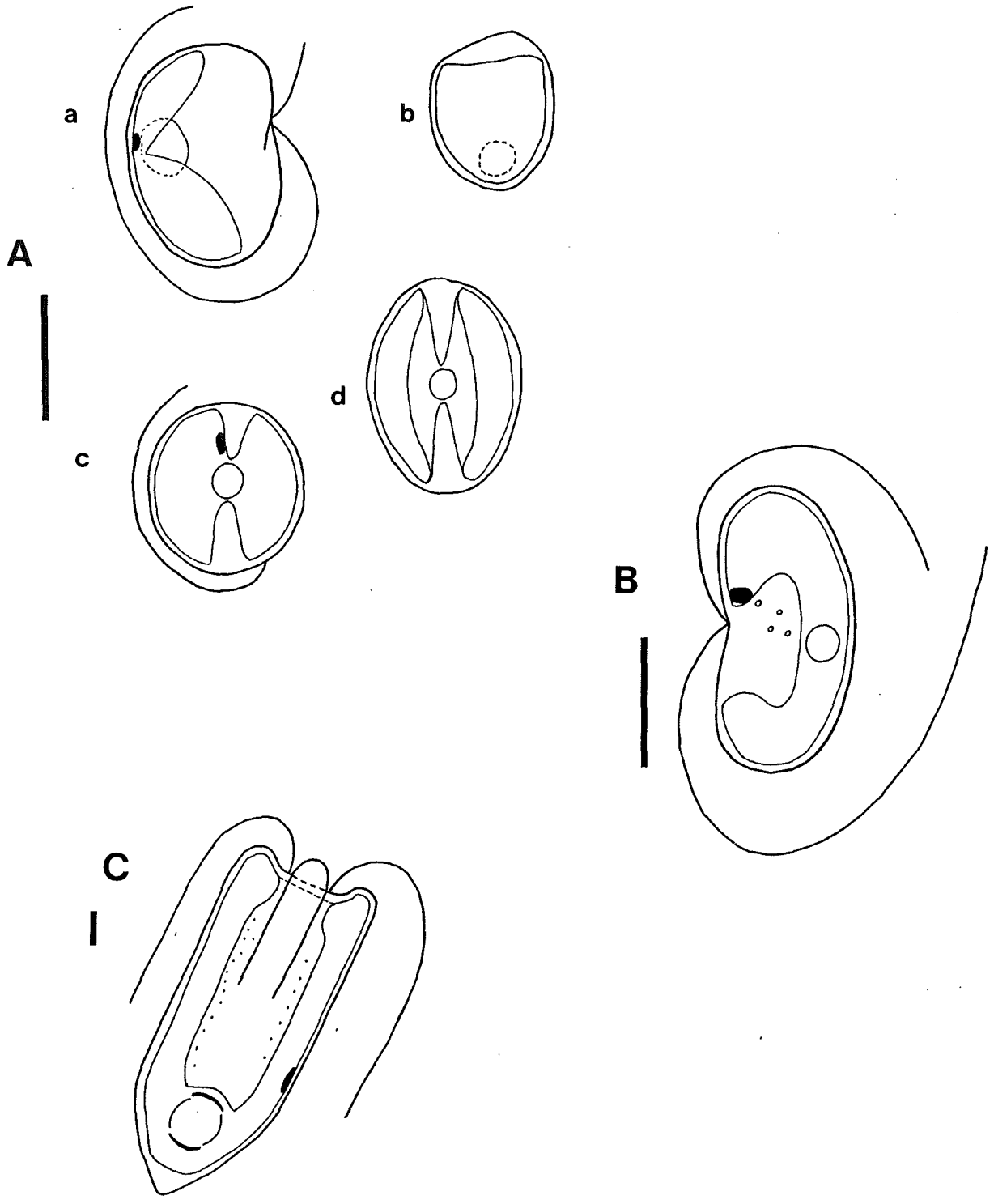

Figure 5/2: Prasinophyceae. A. Mantoniella squamata
a. lateral view b. end view c. bottom view
d. top view; B. Nephroselmis sp.; C. Pyramimonas sp.
Scale 2 µm.

flagella were inserted laterally, towards the anterior end of the cell. The anterior flagellum was 8-12 µm, and the posterior trailing flagellum was 10-14 µm long. Within the cell the lateral chloroplast occupied much of the cell on the side opposite the flagella insertion. An eyespot was prominent at the anterior end of the chloroplast and a large pyrenoid occupied a central position.

It is not possible to further identify this species without electron microscopy to show scale form. Unfortunately the material was sparse within a mixed culture, and attempts at whole mount shadow casting (Moestrup and Thomsen, 1980) or sectioning failed to provide material.

Moestrup and Ettl (1979) provide an excellent treatment of Nephroselmis olivacea, which compares in cell size (slightly wider) with the present material. Another species, N. discoidea has larger, wider cells (Skuja, 1948). Even at the generic level this is a new record for Lake Ellesmere.

Mantoniella squamata (Manton et Parke) Desikachary, 1972
= Micromonas squamata Manton et Parke 1960.

The material from Lake Ellesmere was found in live samples and cultures initiated on 7 July, 1980. The cells were kidney-shaped, 3.5 - 4.5 µm long, and 2.5-3.5 µm wide (Fig. 5/2A). One flagellum was particularly prominent (up to 6.5 times the length of the cell) although on occasions a shorter second flagellum (up to 1.5 µm) was observed. They were laterally inserted. The chloroplast was bi-lobed, with a central pyrenoid opposite the place of flagella insertion. A large eyespot (up to 1 µm) was associated with the chloroplast, on the side away from the flagella.

Electron microscopy of the Ellesmere specimens showed a second flagellum which emerged at an oblique angle to the larger one, but from a similar lateral position. It was difficult to orientate sections to examine both flagella at once. There appeared to be some ultrastructural differences between the two flagella. The longer flagellum had the typical '9 + 2' microtubular arrangement with transition zone into the cell, incorporating a cruciate arrangement and triplets of microtubules. The shorter flagellum was narrower. No central microtubules were found in cross-section, rather only four doublets at some distance from the cell. The transition zone was not observed.

The other features confirmed by electron microscopy were the presence of 'cob-web' type scales on both the cell body and flagella; the pyrenoid and the eyespot. The scales were formed in the golgi apparatus and moved to the cell surface particularly in the region of the flagella. The scales were up to 0.288 μm in diameter. The pyrenoid was observed to be embedded within the chloroplast and was surrounded by starch plates. The eyespot was composed of many closely-packed round spheres, and lay adjacent to the pyrenoid under the chloroplast membrane. It was at least 0.55 μm in diameter.

Recently, Barlow and Cattolico (1980) described Mantoniella squamata in detail from culture. They described the shorter "stubby" flagellum for this organism, which was originally described as uniflagellate. The present material shows that this second flagellum is longer than Barlow and Cattolico suggested, but essentially the same in ultrastructure. The differences in flagellum length may be due to comparison of live and recently cultured material (this study) with long established cultures (Barlow and Cattolico's study).

Further confirmation of the species identity is found in the scale type. Although the 'cob-web' type of scales were found, the other ornamentations of intercalary hair-scales and the distal hairs on the flagellum were not observed.

This record of Mantoniella squamata is new to Lake Ellesmere and New Zealand.

5.3.2 Chlorophyceae

The circumscription of the Chlorophyceae as presented in this section is essentially that of Fott (1971), after the removal of the Prasinophyceae (section 5.3.1). The three orders represented are: Volvocales, Chlorococcales and Ulotrichales.

5.3.2.1 Order 1: Volvocales

This order is not well represented within Lake Ellesmere. Only one genus, Chlamydomonas has previously been reported (Flint, in Hughes et al., 1974). For this present study Chlamydomonas has again been recognised.

Family: Chlamydomonadaceae

Chlamydomonas sp.

Chlamydomonas is a large genus which includes over 450 species (Ettl, 1976). Through lack of adequate material it has not been possible to fully determine the specimens from Lake Ellesmere. The features found are described for future comparison. The cells were spherical to ovate, up to 15 µm in diameter. Two equal flagella emerged from either side of an apical papilla, and were 1-1.5 times the length of the cell. The chloroplast was basal, of the euchlamydomonoid type (see Ettl, 1976 p265), with a basal pyrenoid. An eyespot was present in the anterior end of the cell. The material fits into the Euchlamydomonas group of the genus.

Many species of Chlamydomonas have been reported for New Zealand (Chapman et al., 1957; Flint, 1966; Flint and Ettl, 1966; Sarma and Chapman, 1975).

5.3.2.2 Order 2: Chlorococcales

This order is large and well represented in Lake Ellesmere. It includes the non-motile, unicellular or colonial green algae, some of which lack contractile vacuoles. The cells are generally non-polar at maturity and commonly multiply by autosporulation or rarely by zoosporulation. Sexuality has been demonstrated for some species (Bourrelly, 1966).

This order may be confused with another order, the Tetrasporales, which also have a non-motile dominant phase. The cellular organisation differs, however, having a chlamydomonoid-like cellular organisation with cellular polarity and often possessing contractile vacuoles. Reproduction mostly involves biflagellated cells, of the chlamydomonoid type. Members of the Tetrasporales have not been found in Lake Ellesmere, and will not be treated further.

Pascher (1915) was the first to use the name Chlorococcales based on the type genus Chlorococcum, for the order previously circumscribed as the Protococcales, a name which continued to be applied until 1953 (Korshikov, 1953). The characterization of the order has been widely accepted, although the sub-ordinal arrangement has not received the same acceptance. This is illustrated in the number of families presented by different authors. Smith (1950) and Bourrelly (1966) recognize 10 families, whereas Fott (1971) has 16 and Prescott (1951) has 8. Those families that are most readily accepted

are often smaller and form more natural groupings, for example Scenedesmaceae, Micractiniaceae, Hydrodictyaceae and Dictyosphaeriaceae. The large groupings of families are rearranged according to the key characters chosen by the various authors, and can therefore be considered as unnatural. These unnatural families would include Oocystaceae sensu Bourrelly (57 genera), sensu Fott (11 genera); and Chlorococcaceae sensu Bourrelly (45 genera), sensu Fott (6 genera). This would confirm that at least part of the order is not a natural grouping, but rather an assemblage of genera grouped together because of a simple resemblance (Bourrelly, 1966).

A more recent treatment (Bold and Wynne, 1978) has separated the coccoid green algae into those that have motile zoospores and/or gametes, the Chlorococcales; and those that reproduce only by autospores, the Chlorellales. This reduces the Chlorococcales to four families, three which are unicellular and the fourth coenobial; and the Chlorellales, with only two families: the Chlorellaceae and the Scenedesmaceae. Such a separation between the orders implies that there is a crucial significance in the presence or absence of a flagellated stage in the life history. A similar arrangement, with the separation at the subordinal level, is found in Brunnthaler (1915). At that time, the suborders were recognised as Zoosporinae and Autosporinae. Brunnthaler has been criticized (Starr, 1954; Philipose, 1967), as Bold and Wynne should be for the erection of an order using a variable feature. From within the Chlorococcales sensu Fott, or sensu Bourrelly, there are several examples of genera having flagellated cells in one species and not in another. The existence of these problem genera suggests that the character of zoosporulation/autosporulation is variable. Starr (1954) found both zoospores and autospores formed in Tetraedron bitridens when cultures were in an active vegetative condition. Other species of Tetraedron have been known to only reproduce by autospores, although zoospores were postulated for T. minimum by Probst (1926, not seen; cited by Starr, 1954). In the genus Dactylosphaerium, a little known genus in the Dictyosphaeriaceae, there has been zoosporulation noted for only one species (Hindák, 1977). This report needs to be confirmed and the structure of the zoospores recorded. In Dictyosphaerium indicum the occurrence of oogamy is widely accepted (Iyengar and Ramanathan, 1940; Komárek and Perman, 1978). In this rare

species, autosporulation also occurs, whereas other species of Dictyosphaerium have only been observed to reproduce by autospores (Komárek and Perman, 1978). The final example comes from Scenedesmus, a widely studied genus, which is not without taxonomic problems (Hindák, 1979). However, for the present, only the reproductive method is of concern. Most species are known to reproduce by autosporulation; but Trainor and Burg (1966) reported flagellated cells in S. obliquus and S. dimorphus. Flagellated cells were released in a low nitrogen medium, and these were supposed to be gametes because parthenogenetic development (i.e. zoosporulation) did not occur, but conjugation was not observed in this case. Uncertainty as to the function of the motile cells remains, but the release of the flagellated cells must be significant. Pickett-Heaps (1975) showed that in the autocolony formation in other species of Scenedesmus the new cell walls of adjacent cells formed before release of the colony.

These examples taken from widely different parts of the order Chlorococcales sensu Bourrelly, or sensu Fott, indicate that the method of reproduction can vary. Consequently, it would be unwise to separate genera into two separate orders on the basis of reproduction as did Bold and Wynne (1978) with Chlorococcales and Chlorellales, until more species have been investigated in a wide range of conditions.

The present study will therefore take a broad circumscription of the order Chlorococcales and follow the arrangement presented by Fott (1971), dealing only with the families present in Lake Ellesmere. It is at the family level that the natural and unnatural groupings are often recognised. It is therefore worthwhile to directly compare the included families.

(1) Family: Botryococcaceae

Mucilaginous colonies, with cells held at the periphery of radial extensions of the mucilage. A small family, with 2 genera.

(2) Family: Dictyosphaeriaceae

Colonial organisms, cells connected by the remnant mother-cell wall. A family including about 12 genera.

(3) Family: Oocystaceae

Solitary or colonial organisms; if colonial, non-coenobic and irregular. Reproduction by autosporulation. A large family, which is largely unnatural, with several distinct groups considered as sub-families, including Ankistrodesmoideae.

(4) Family: Scenedesmaceae

Colonial organisms, with coenobial form. Coenobia with 4, or multiples of 4 cells. Reproduction largely by autosporulation.

Family 1: Botryococcaeae

This family is often included within the Dictyosphaeriaceae (Bourrelly, 1966), but it can be separated on the colony form (Fott, 1971). The cells are peripheral in the colony and are enclosed within radial extensions of the colonial mucilage. The family has only two genera, Botryococcus Kützing and Botryosphaera Chodat, distinguished by the shape of their cells, ± pyrenoid, and the shape of the plastid (Bourrelly, 1966).

Genus: Botryococcus Kützing 1849:892

Botryococcus has had a varied history. First included within the Palmellaceae (Kützing, 1849), it was subsequently listed within the Tetrasporeae (Klebs, 1883, not seen; cited in Blackburn, 1936) and Xanthophyceae (Pascher, 1939; Fritsch, 1935). The recognition of starch within the cell (Blackburn, 1936), and more recently the identification of chlorophyll b (Belcher and Fogg, 1955), finalized its position within the Chlorophyta and Chlorococcales. The genus has two or three species (Bourrelly, 1966), which are widely distributed in planktonic waters. Two species have been identified for New Zealand, B. braunii Kützing and B. protuberans West and West (Cahpman et al., 1957; Flint, 1966). Only B. braunii has been identified from Lake Ellesmere.

Botryococcus braunii Kützing, 1849:892

(Fritsch 1935: 476; Blackburn 1936:842; Belcher and Fogg, 1955:81)

Of cosmopolitan distribution, within New Zealand first reported for Lake Sarah (Flint, 1938); but widespread in lakes of all trophic

levels (Flint, 1975), including Lake Ellesmere (Flint, in Hughes et al. 1974).

Botryococcus braunii is distinguished from B. protuberans by the extent to which the cells project from the colonial mucilage. In B. protuberans, the cells project prominently from the mucilage (Fritsch, 1935).

Botryococcus braunii was found in samples from Lake Ellesmere throughout the study period. It was most often near the surface of the water column due to the buoyant nature of the colony. Net sampling enabled concentration of the organism and isolation (net sample 12/02, 28 May, 1979). B. braunii was not counted in plankton samples, owing to the small population size and the buoyancy of the colony.

Family 2: Dictyosphaeriaceae

A larger family than the preceding Botryococcaceae. The Dictosphaeriaceae sensu Fott (1971) includes the colonial organisms in which the remnant mother cell wall connects the cells. Reproduction within the family is by autospores in which the fragmentation of the cell wall releases the daughter cells. These cells remain attached to the mother cell wall, which may be modified to form thick strands (Komárek and Perman, 1978). The attachment of the daughter cells is characteristic of the individual genera (Hindák, 1977). Colonial mucilage is frequently present, and this may be amorphous or structured (Bourrelly, 1966).

This family, sensu Fott, has about twelve or thirteen genera, several of which have few species. Bourrelly's (1966) circumscription incorporated Botryococcus. The genera previously recorded for New Zealand are Dimorphococcus and Westella (both included as Oocystaceae), Dictyosphaerium (Chapman et al. 1957), Dictyochlorella and Quadricoccus (Thomasson, 1974).

Genus: Dictyosphaerium Nägeli 1848:73.

Dictyosphaerium is described and separated from other genera within the family on account of the form of the colony. The autospore production results in 4 autospores (or sometimes 2) attached to the ends of the mucilaginous stalks, which are transformed flaps of the mother cell wall (Komárek and Perman, 1978).

Closely related genera include: Quadricoccus, distinguished by the colony being flat or cupshaped, with oval cells on the margin (Komárek and Perman, 1978); Dactylosphaerium distinguished by the less regular nature of the mucilage strand ramification (Hindák, 1977); and Dimorphococcus with 2 cell types according to position within the colony (Bourrelly, 1966).

Komárek and Perman (1978) have reviewed the genus recently, and it is intended to follow their determination for the present taxonomy. Three species were recognised Dictyosphaerium ehrenbergianum, D. pulchellum and D. primarium. All three have been recorded previously for Lake Ellesmere (Flint, in Hughes et al., 1974). Within New Zealand, a fourth species has previously been identified, D. planctonicum (Thompson, unpublished, in Chapman et al., 1957). However, this species was excluded from the genus by Komárek and Perman (1978: 282) and given as synonymous with Lobocystis dichotoma Thompson.

Dictyosphaerium ehrenbergianum Nägeli

(Komárek and Perman, 1978: 272)

Commonly distributed in Northern temperate regions (Komárek and Perman, 1978). For New Zealand, first identified by Flint for Lake Sarah (Flint, 1938); Cassie (1969) for Lakes Rotorua and Ohakuri, and Thompson (Chapman et al., 1957) for Albany.

Dictyosphaerium ehrenbergianum is characterized by the ovoid cells attached with their longer sides to the stalks (Komárek and Perman, 1978). The other species so attached is D. elongatum, which has larger colonies, and cells that are lengthy-reniform to narrow oval, and noted for being distinctly asymmetric (Hindák, 1977).

The material from Lake Ellesmere was variable, falling somewhere between the two species mentioned above, but closest to D. ehrenbergianum. The cell sizes were 3-4 µm by 8 µm, which are a little narrower than given for D. ehrenbergianum by Komárek and Perman (1978), and yet wider than D. elongatum. The cells only occasionally tended towards reniform, and they were always asymmetric. The colony size was most often less than 8 cells, frequently 4 cells close together, with wide mucilage strands. Because of the small colony size, it was not possible to distinguish whether the colonial mucilage formed around quadruples of cells.

The distinction between the two species is inadequate on the basis of the present material. In view of the closeness of cell size

ranges and the similar attachment mode, there may be some doubt as to the validity of Hindak's new species D. elongatum. The present material suggested a range of cell shapes (reniform to ovoid) may exist, along with a variation in colony size and colonial mucilage production.

Dictyosphaerium ehrenbergianum was found in the plankton of Lake Ellesmere for the whole of the study period, but was more abundant in summer periods.

Dictyosphaerium pulchellum Wood

(Komárek and Perman, 1978:254)

Widely distributed from the subarctic to the tropics, especially in temperate zones (Komárek and Perman, 1978), in New Zealand it was recorded for the first time by Thompson for the Waikato River (Chapman et al., 1957). It was unfortunate that Flint (1975) did not separate the various species of Dictyosphaerium when comparing the large number of local lakes, but D. pulchellum has however been previously reported for Lake Ellesmere (Flint, in Hughes et al., 1974).

Dictyosphaerium pulchellum cells are large and spherical, ranging 5-8 µm. Colonies can be quite large, frequently up to 32 (-64) cells. The cells are of the chlorelloid type with the attachment of the mucilage strand at the location of the chloroplast containing the pyrenoid (Komárek and Perman, 1978). The other species with spherical adult cells are distinguished by the cell size, ±pyrenoid, and cell wall granulations. The most similar (i.e. with one pyrenoid, smooth cell wall) are D. primarium and D. chlorelloides. These two species differ from D. pulchellum because of the cell size and number of cells in the colony. D. primarium has cells 1.5-3 µm, up to 32 per colony, often close together and thin mucilaginous strands. The cell size is less than, and does not overlap with the range of D.pulchellum var. minutum Delf. the smallest variety recognised by Komárek and Perman (1978). D. chlorelloides (Naumann) Komárek et Perman was combined for the small colonies (2-4 cells) with cells 3.8 - 6 (-7) µm. The cells were distant from each other, with colonial mucilage around individual cells. There is a marked overlap in cell sizes, and without other distinguishing features some doubt may be placed on this species.

The material determined as D. pulchellum for Lake Ellesmere was mostly colonial, with the evident mucilaginous strands connecting cells (Fig. 5/3B). The cell sizes were up to 7 µm for unicells, and

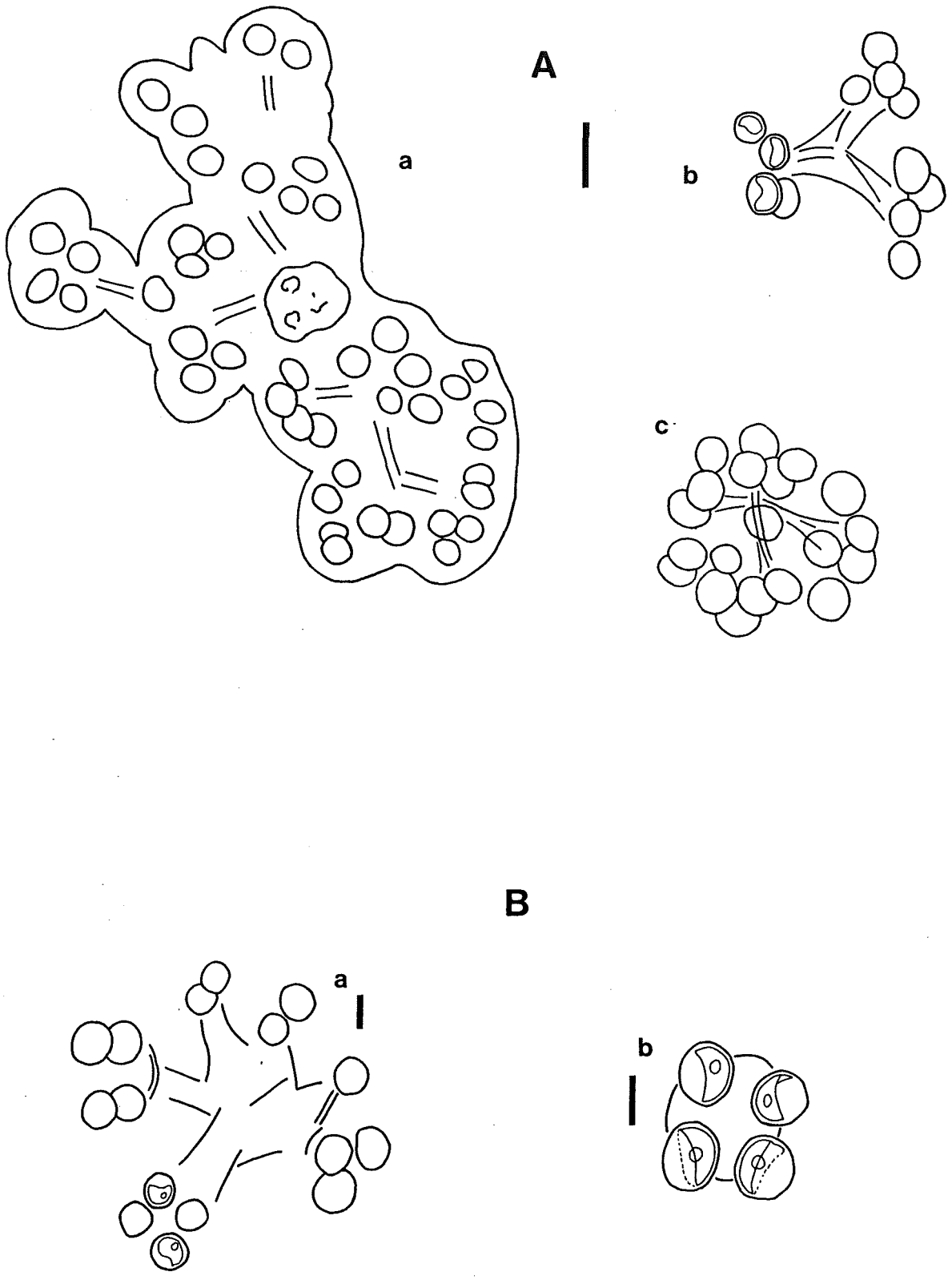

Figure 5/3: Chlorophyceae A. Dictyosphaerium primarium.
a. large colony with thick colonial mucilage.
b-c small colonies without colonial mucilage;
B. Dictyosphaerium pulchellum a colony
b. autospore release .
Scale 5 µm.

diminished to 5 µm for cells within colonies. Cells were spherical, and autospores immediately after division were ellipsoidal.

There was potential confusion between preserved unicells of Dictyosphaerium pulchellum and Chlorella vulgaris, since the cell morphology and size coincided. In the counting procedure, unicells were frequently referred to as Chlorella, whereas colonies were recorded as Dictyosphaerium. The extent of error was not thought to be great, because of the greater proportion of colonies.

Dictyosphaerium primarium Skuja 1964:137

(Skuja 1956:181 (= D. simplex Skuja, non D. simplex Korshikov); Komárek and Perman 1978:251)

Distributed in plankton of slightly eutrophic reservoirs from both Sweden and Czechoslovakia (Komárek and Perman, 1978). Reported for New Zealand from Lake Ellesmere (Flint, in Hughes et al., 1974).

Dictyosphaerium primarium is one of the two species of the genus with small cells. The adult cells are spherical, up to 3 µm in diameter. They can be distinguished from the similar sized species, D. botrytella by the presence of a pyrenoid and by their cells which are spherical, rather than being oval to almost spherical. The pyrenoid is often difficult to observe (Skuja, 1956). Release of autospores from the mother cell is also by a different method (Komárek and Perman, 1978). In D. primarium, the cells are more or less distant from one another and attached to their nearly invisible stalks. Colonial mucilage is colourless and difficult to view unless stained. These two species, D. primarium and D. botrytella are very similar and the most positive basis on which to separate them is the presence or absence of the pyrenoid.

Samples were collected from Lake Ellesmere throughout the whole of the study period (Fig. 5/3A). The colonies were variable in size, up to an estimated 45 cells. The cells were close together, and mucilaginous strands were rarely visible. Colonial mucilage was variable, sometimes absent, but during a period from late summer into autumn 1979 thick colonial mucilage was very evident. The cells were spherical, about 2 µm, never larger than 3 µm. A pyrenoid was seen in some of the material.

The observation of a pyrenoid suggested D. primarium was the most appropriate determination. The colonies observed were occasionally

larger than described by Komárek and Perman (1978). This species was dominant within Lake Ellesmere for much of the collection period.

Genus: Lobocystis Thompson 1952

A single species of Lobocystis was first identified in the United States: L. dichotoma. The cells were ellipsoidal (8-13 µm by 5-8 µm). Reproduction occurred through the formation of two autospores. Colony formation occurs through the retention of the cells within the mother cell wall, which swells in a divergent manner.

Bourrelly (1966) described a new variety from Europe, Lobocystis dichotoma var. mucosa, which was distinguished from the rest of the species by smaller cell sizes (6-7 µm by 2.5-3 µm), and by the presence of colonial mucilage. Other reports of L. dichotoma var. mucosa since the original description show the same swelling of the mother cell wall, and the subsequent breakdown to form narrow strands (Williams, 1972; Kling, 1981).

Lobocystis ?sp. nov.

Cells elongate - ellipsoidal to cylindrical with rounded ends, 5-8 µm long, 2-3 µm wide (Fig. 5/4). Colonies of up to 30 cells, although most were smaller. It reproduces by means of two autospores, which are released from opposite ends of the mother cell. Autospores remain attached to the ends of the remnant mother cell wall, with subsequent division. Occasionally the second cell division occurs in one or both of the autospores before the autospores are released from the mother cell. In this case, they separate upon initial release. Within each cell there is a large central band shaped chloroplast, with a single central pyrenoid. In some cells there is a terminal vacuole-like space which may or may not contain granules. No colonial mucilage has been seen.

The features which distinguish this species from others described for Lobocystis are the size of the cells (similar to L. dichotoma var. mucosa), the lack of colonial mucilage (similar to L. dichotoma), the manner of release of the autospores and the nature of the remnant mother cell wall (different from both taxa). In L. dichotoma the autospores are retained within the mother cell wall "which swells in a divergent manner and which adheres to the rupture orifice of the previous cell generation" (Thompson, 1952:366). In the case of

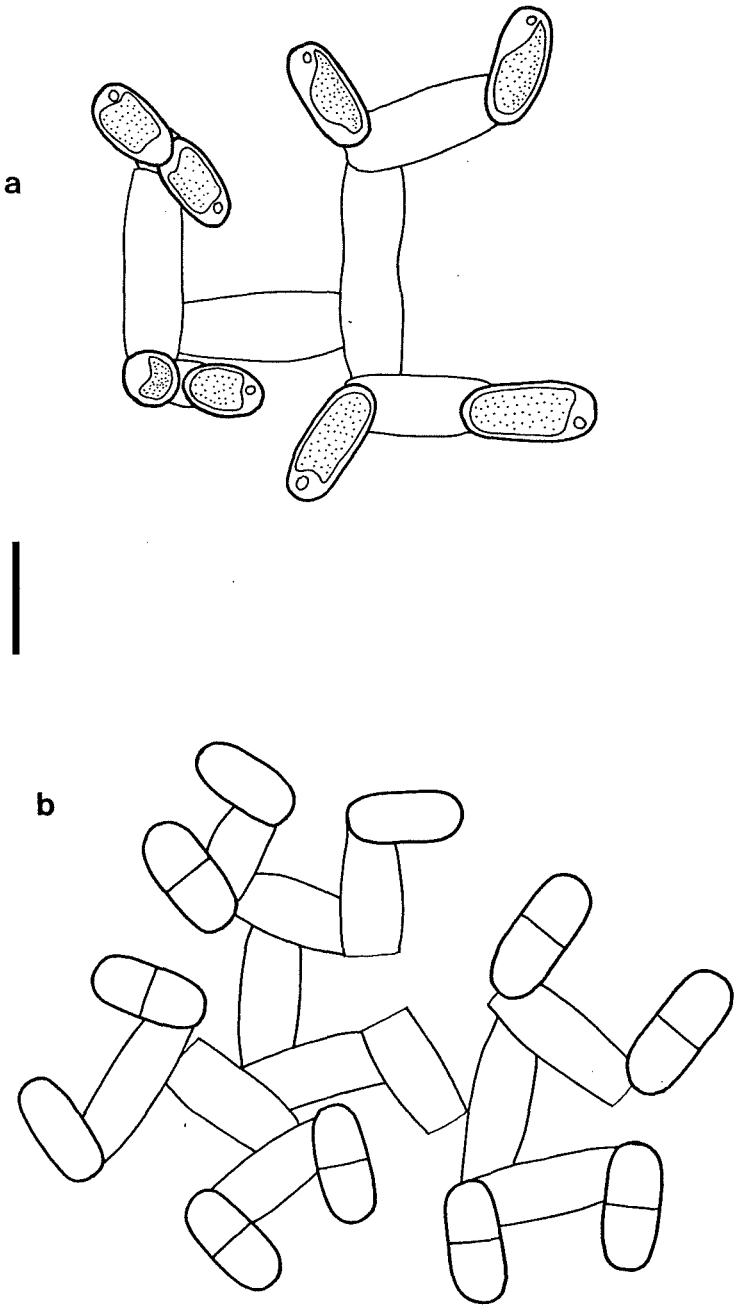

Figure 5/4: Chlorophyceae. Lobocystis sp.nov. a-b colony form. Scale 5 µm.

L. dichotoma var. mucosa this swelling of the mother cell wall is not mentioned by observers, but Bourrelly illustrates it (Bourrelly, 1966, Plate 34, Fig. 1). In both of the above taxa the breakdown of the remnant mother cell walls occurs during the formation of strands within the colony.

This material differs markedly from the two other taxa in respect to these aspects relating to the mother cell wall. The mother cell wall does not swell in this organism to the same degree, if at all, and the remnant wall remains very close to the size of the vegetative cell. This remnant wall persists for several cell generations and thus the colony structure is formed. Unlike the other taxa its cell wall does not narrow and form strands within the colony. This feature may in fact exclude the present material from the genus Lobocystis. However the similarity between all three taxa suggests that emendment of the genus is necessary. Another related genus within the Dictyosphaeriaceae which produces 2 autospores, and has elongated cells (as opposed to spherical cells) is Dichotomoccus. Until recently it was thought to belong to the Xanthophyceae (Komárek, 1964), but Hindák (1978) has now shown the presence of chlorophyll b. The present material is unlikely to belong to Dichotomococcus because of the presence of a pyrenoid within the single chloroplast. Dichotomococcus species lack pyrenoids and have one to many chloroplasts.

Komárek (pers. comm. to Dr E.A. Flint, 2 January, 1980) suggests the present material may belong to a new genus, in which he would also include "Lobocystis dichotoma var. mucosa". However in view of the form of the remnant mother cell wall outlined above, this view is not accepted in this study. Williams (1972) also lists cell sizes wider than the present material or for other descriptions of variety mucosa. None of the reports of Lobocystis dichotoma (Hortobágyi, 1969; Guarrera et al., 1972; Balakrishnan and Rao, 1977; Cardinel, 1979) show the same structure of remnant cell wall as the present material, although some of the cell sizes would indicate the identity as L. dichotoma var. mucosa, rather than L. dichotoma.

The resolution of this taxonomic problem must be either to recognise this material as different from any other species previously described, and to include it within an emended genus Lobocystis, or

alternatively to erect a new genus for this organism. This new genus would be positioned close to both Lobocystis and Dichotomococcus, within the family Dictyosphaeriaceae.

Lococystis ?sp. nov, as described above was found within Lake Ellesmere for most of the study period. Although not a dominant organism, it was often present in moderate numbers.

Family 3: Oocystaceae

The Oocystaceae is a large family within the Chlorococcales. It includes those organisms that are solitary or free within colonies not forming definite coenobia; reproduction is only by autosporulation (Bourrelly, 1966; Fott, 1971). To a large extent this is not a natural group, but a composite of simple forms, just as the Chlorococcaceae includes solitary forms that reproduce by zoospores. Fott (1971) separated sub-families using several different characters, including enlargement of the cell wall at the time of autosporulation; mucilage formation; possession of setae and cell shape.

Bourrelly (1966) had used a wider circumscription than Fott (1971) and included 57 genera within the family. Fott separated off those genera with fusiform cells into the Ankistrodesmaceae and the genus Eremosphaera into its own family because of the chloroplast type and oogamy. Fott (1971) will be largely followed in this treatment, with the inclusion of the Ankistrodesmoideae as another sub-family.

The members of this family are particularly important planktonic organisms and are often found in eutrophic waters (Fott, 1971; Cassie, 1979). The Oocystaceae are well represented in New Zealand and also an important group in Lake Ellesmere (Chapman et al., 1957[1]; Flint 1966; Sarma and Chapman, 1975; Flint, in Hughes et al., 1974). The sub-family arrangement follows Fott (1971), with the addition of Ankistrodesmoideae. Each sub-family is represented.

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[1]Chapman et al. (1957) claim to follow Fritsch (1935) in arrangement of the families, but in fact they have included genera from Oocystaceae sensu Fritsch (Oocystis, Nephrocytium), Selenastraceae sensu Fritsch (4 genera), Chlorellaceae sensu Fritsch (3 genera), Dictyosphaeriaceae sensu Fritsch (2 genera) and Eremosphaeraceae (1 genus).

1. Sub-family: Chlorelloideae.
   Cell wall smooth or warty, at autosporulation only slightly enlarged.
2. Sub-family: Lagerheimioideae
   Cell wall with long spines.
3. Sub-family: Oocystoideae
   Cell wall smooth or warty, at autosporulation cell wall enlarged or gelatinous.
4. Sub-family: Ankistrodesmoideae
   Cell wall ruptures or gelatinizes to release autospores.
5. Sub-family: Tetraedronoideae
   Cells 3-5 sided, flat or tetrahedral.

Sub-family 1: Chlorelloideae

This sub-family is distinguished from others within the family Oocystaceae in the simple arrangement of its cells. The mother cell wall does not expand conspicuously prior to the release of the daughter cells, and the autospores are released by cell wall rupture or gelatinization (Hindák, 1977). The cells are for the most part solitary and not retained after autosporulation.

The genera within this sub-family are distinguished by their cell shape and the presence or absence of a warty cell wall. The most common and widespread genus is Chlorella, with spherical cells, and smooth cell wall.

Genus: Chlorella Beijerinck

The genus Chlorella is of importance within the green algae because of the simple unicellular cells which belong to a very simple life cycle. Recently, Fott and Nováková (1969) have monographed the freshwater species of the genus and shown that morphological and structural details were not easily distinguished. The small size of the cells in Chlorella put it near the limit of resolution of the light microscope; however, Fott and Nováková compared several culture strains on morphological grounds, with physiological and biochemical properties applied at the infraspecific level. Nine species were recognised within the monograph and it is proposed to follow this taxonomy.

Chlorella has spherical, subspherical or ellipsoidal cells, with a smooth cell wall without mucilage; cells are solitary or in small irregular groups. The chloroplast is single, parietal, covering nearly the whole of the periphery of the cell or only part of it, with or without a pyrenoid. Reproduction is by autospores, which are released by rupture or dissolution of the mother-cell wall. (Fott and Nováková, 1969).

Several species of Chlorella have previously been recorded for New Zealand (Chapman et al., 1957; Sarma and Chapman, 1975; Cassie and Freeman, 1980). For Lake Ellesmere, the genus has previously been recorded (Flint, in Hughes et al., 1974).

One species has been determined from this study: Chlorella vulgaris.

Chlorella vulgaris Beijerinck

(Fott and Nováková 1969:20)

Cells ellipsoidal to spherical, mother-cell approximately spherical. Chloroplast cup-shaped or girdle-shaped, with an irregular aperture. Pyrenoid distinct. Reproduction by 2-16 autospores. Fragments of the mother-cell elongated or irregular persisting in the culture medium. Dimensions: cells 2-10 µm. (Fott and Nováková, 1969).

This species is widely distributed in water, soil and aerial habitats, and has previously been reported for New Zealand (Chapman et al., 1957). It is now reported for Lake Ellesmere.

The material from Lake Ellesmere was noted in live and preserved samples, and was isolated by culture technique. The cells were spherical with a cup-shaped plastid, and large spherical pyrenoid in the basal region (Fig. 5/5A). Cell sizes ranged 4-6 µm, with smaller autospores. The autospores were more or less ellipsoidal, 4 from each mother cell.

During the counting procedure, there was some confusion between Chlorella vulgaris and unicells of Dictyosphaerium pulchellum. Unicells were frequently recorded as Chlorella. This source of error was not thought to be very great.

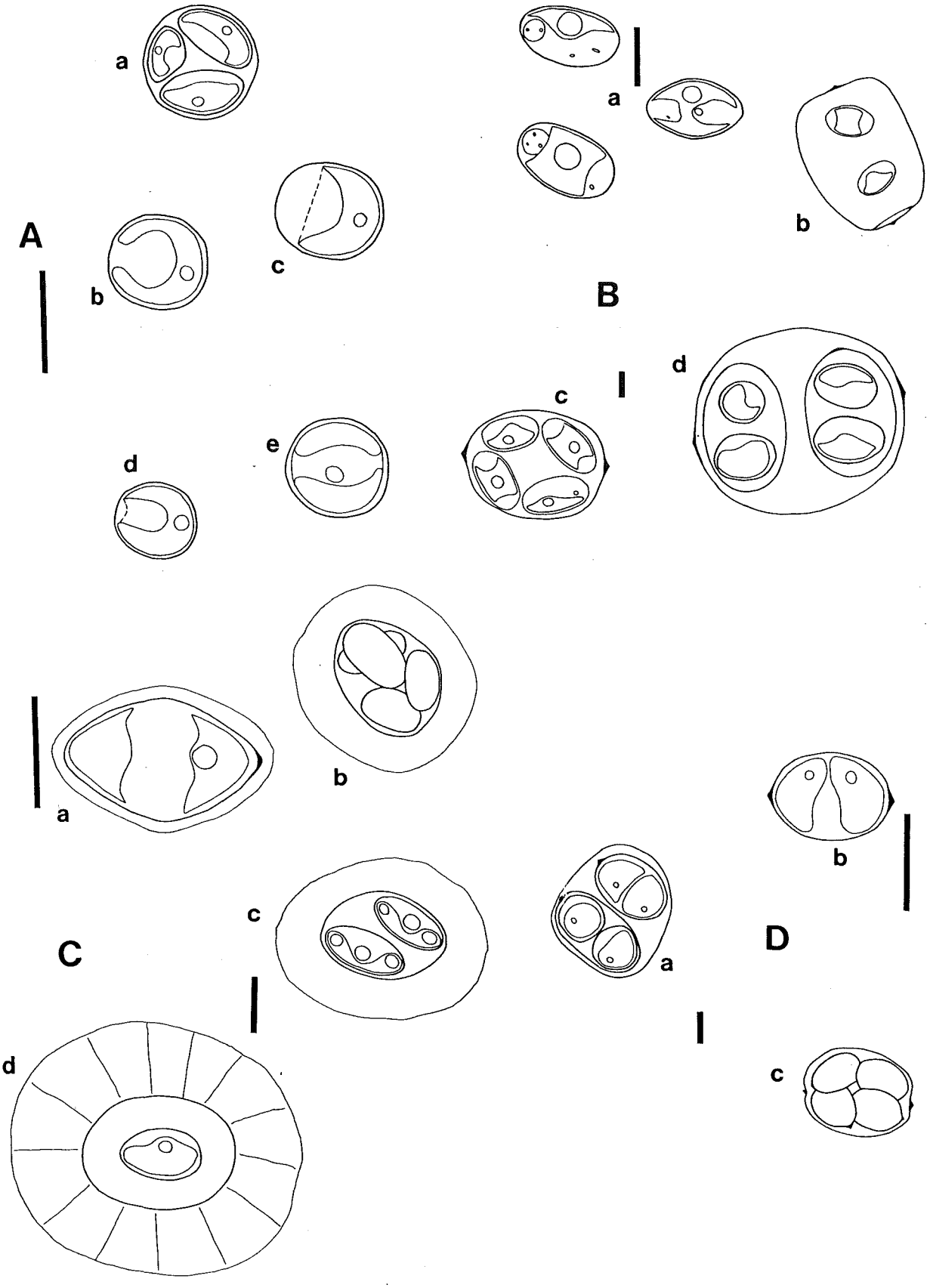


Figure 5/5: Chlorophyceae A. Chlorella vulgaris a. autospore formation b-e vegetative cells; B. Oocystis parva a. autospores b-d colony form; c. Oocystis lacustris a. autospore b-d colony form; D. Oocystis marssonii a&c colony form. b. autospore. Scale 5 µm.

Sub-family 2: Lagerheimioideae

This sub-family of the Oocystaceae includes the members with long setae on the cell wall. Three genera are most common and are distinguished according to the presence or absence of a swelling at the base of the setae, and also the distribution of the setae around the cell (Fott, 1971).

There has been much confusion regarding two of the genera within this sub-family: Lagerheimia Chodat and Chodatella Lemmermann. Lagerheimia was originally described in 1895, and Chodatella was separated in 1898 on account of the absence of a swelling at the base of the setae. This distinction was accepted by Brunnthaler (1915), and Fritsch (1935), but not accepted by Printz (1927), Smith (1920, 1933) and Korshikov (1953).

In 1948 two monographs were produced on the genus Lagerheimia. Ley (1948) dismissed the name Lagerheimia as invalid on the grounds that Saccardo (1892) had used it earlier for a fungal genus. He therefore transferred all the species to Chodatella as the most valid name. Smith (1950) and Bourrelly (1966) follow this arrangement in recognising one genus: Chodatella. Skuja (1956) and Philipose (1967) consider Ley to be in error in considering Lagerheimia Chodat invalid, since Saccardo used the name Lagerheima not Lagerheimia. Boedijn (1940) also recognised the similarity of names, from a fungal point of view, and erected the name Lagerheimiella for the algal genus. Yet if the phonetically similar name is rejected, the earlier name Bernardia Playfair (1917) would have priority over Lagerheimiella Boedijn, provided the circumscription distinguished Chodatella Lemmermann as a separate genus.

Fott (1948) also monographed the genera Chodatella and Lagerheimia, and considered that they could both be upheld. Fott emended the description of Chodatella so that it included only species with polar and/or equatorial setae, without basal swellings and the setae formed after the release of the autospores.

The genera and species of this sub-family reflect the difficulties of the taxonomy as discussed. This account accepts the view of Fott in differentiating Lagerheimia (this name retained until a case against the phonetically similar name is made), Chodatella and Franceia.

Records for New Zealand, including Lake Ellesmere, need careful arrangement due to the synonymy created by Ley in transferring all Lagerheimia species to Chodatella. The species of the Lagerheimioideae recorded for New Zealand include:

Lagerheimia chodati Bernard, by Flint (1966)
(claimed as first find by Flint - as "L. chodatii")
= Bernardia chodati (Bernard) Playfair, by Playfair (1917) (not previously noted in checklists).

Chodatella ciliata (Lagerheim) Lemmermann
= Lagerheimia ciliatia (Lagerheim) Chodat, by Thomasson (1974) (as "Lagerheimia ciliata (Lagerh.) Lemm.").

Chodatella citriformis Snow, by Cassie and Freeman (1980)
(incorrect authority "C. citriformis (Snow) G.M.S.", also incorrectly claimed as first record).
= Lagerheimia citriformis (Snow) G.M. Smith, by Thomasson (1960).

Chodatella quadriseta Lemmermann, by Cassie (1978)
= Lagerheimia quadriseta (Lemmermann) Smith, by Flint (in Hughes et al., 1974)(as "L. quadriseta Lemm.")

Chodatella subsalsa (Lemmermann) Lemmermann, by Flint (1975)
= Lagerheimia subsalsa Lemmermann, by Haughey (1968).

Diacanthos belanophorus Korshikov, by Haughey (1968) and Cassie (1978) (as "Dicanthos").

Franceia ovalis (Francé) Lemmermann, by Flint (in Hughes et al., 1974) (not previously noted in checklists).

Only the genera Chodatella and Franceia will be considered in this account.

Genus: Chodatella Lemmermann emend. Fott 1948:11

Following the emendment of this genus by Fott, the diacritical characters may be regarded as the possession of four to more setae, which are only subpolar, or subpolar and equatorial, but never covering the whole surface of the cell (compare Franceia). The setae are fine or firm without a swelling at the base (compare Lagerheimia) (Fott, 1948).

The characters used to separate the species revolve around the cell shape, the presence of equatorial setae, and the length and number of subpolar setae.

Four species have been previously recorded for New Zealand: C. citriformis (Cassie and Freeman, 1980; Thomasson, 1960 as Lagerheimia citriformis), C. quadriseta (Cassie, 1978; Flint, in Hughes et al., 1974 as Lagerheimia quadriseta for Lake Ellesmere), C. subsalsa (Flint, 1975; Haughey, 1968 as Lagerheimia subsalsa), and C. ciliata (Thomasson, 1974, as Lagerheimia ciliata).

Chodatella quadriseta Lemmermann 1898b: 310

(Brunnthaler 1915: 139; Fott 1948: 20; Philipose 1967:169)

= Lagerheimia quadriseta (Lemm.) G.M. Smith 1926:180

(Prescott 1962:251)

Cells ellipsoidal to subglobose to nearly spherical, with two subpolar setae at each end. Usually the setae are in one plane and straight, but sometimes the planes of each pair of setae are crossed and the setae may be slightly curved. Length of cells 5.5-12 µm; breadth 3.5-8 µm; setae length 11-23 µm.

Distribution: Cosmopolitan in ponds, rivers and lakes of Europe, Asia (Siberia), Africa (Lake Victoria), North and South America, with varieties in Australia, China and Yugoslovia (Fott, 1948); India (Philipose, 1967). For New Zealand, in Lake Ellesmere (Flint, in Hughes et al. 1974, as Lagerheimia quadriseta); Lakes Rotoiti and Rotoehu (Cassie, 1978); and Lake Waikere (Cassie and Freeman, 1980).

Chodatella quadriseta was found in samples throughout the study period, and was more common than C. subsalsa. The average size of the cell was within the range given for the species (length = 10 µm; breadth = 5 µm), with smaller cells noted in winter 1980 (length = 5 µm; breadth = 3 µm). The setae were usually about the length of the cell, and as such were marginally shorter than previously reported for this species. The setae were most often orientated in the same plane, although occasionally at right angles at different ends of the cell.

Chodatella subsalsa (Lemmermann) Lemmermann 1898b:310

(Brunnthaler 1915:139; Fott 1948:19)

= Lagerheimia subsalsa Lemmermann 1898a

(Smith 1920:130; Prescott 1962:251)

Cells ellipsoidal to oval, usually with (2)-3-(4) sub-polar setae at each end. Length of cells 5-12 µm; breadth 2.5-8 µm, length of setae 7.5-20 µm. This species is differentiated from the previous

one by the number of sub-polar setae, usually three.

Distribution: Cosmopolitan, in ponds, rivers, water supplies, including brackish water; in Europe, Asia (Java), Africa, North America, Australia (Fott, 1948). For New Zealand, in Mangere Oxidation ponds (Haughey, 1968 as Lagerheimia subsalsa), Lakes Pearson, Ida and Tripp (Flint, 1975).

Chodatella subsalsa was less common in Lake Ellesmere than C. quadriseta, and was mostly found in spring to autumn samples. The cell sizes were similar to C. quadriseta, fitting within the range given by Fott (1948) (length = 10-12 µm; breadth = 5 µm; setae = 10 µm). Autospores before their release, lacked setae, and were about 8 µm long. The arrangement of the setae was a little variable, but usually was an opposite tetrahedral arrangement with six setae. Some cells had different numbers of setae at each end (2 and 4); and although unusual for this species, they were not consistent enough to fit into another species (C. balatonica or C. playfairii).

Genus: Franceia Lemmermann 1898b: 307

This genus differs from Chodatella in having setae covering the entire cell wall and also the cells may be aggregated in small colonies (Smith, 1950; Fott, 1971). The setae are numerous and evenly thin throughout their length (Fritsch, 1935).

This genus has about eight species which are of wide distribution. The only member recorded for New Zealand is Franceia ovalis for Lake Ellesmere (Flint, in Hughes et al., 1974).

This genus has wide acceptance, but its similarity to other thin setae bearing genera suggests the need for careful investigation. Golenkinia which is at least superficially similar with spherical cells, is usually placed in the Micractiniaceae, a family where some members produce by zoospores (Philipose, 1967).

Franceia ovalis (Francé) Lemmermann 1898b: 308

(Smith 1920: 131; Prescott 1962: 251)

Cells ovoid to elliptical, with 1-2 chloroplasts. Cells 13-17 µm long; 7-10 µm wide; setae 15-23 µm long. Distribution: Europe (Lemmermann, 1898b); North America (Smith, 1920; Prescott, 1962). In New Zealand, recorded for Lake Ellesmere (Flint, in Hughes et al., 1974).

This is a rare organism and only ever found in plankton (Brunnthaler, 1915; Prescott, 1962).

In this present study, it has been recorded in live plankton samples, showing small cell sizes. It has not been in sufficient numbers to be counted.

Sub-family 3: Oocystoideae

The sub-family Oocystoideae includes the solitary or colonial autosporine chlorococcal algae, the cell wall of which expands conspicuously when the autospores are developed (Hindák, 1977). The cell wall of the cells is smooth or warty and is without setae (Philipose, 1967; Fott, 1971).

The Oocystoideae are distinguished from the Chlorelloideae by the expansion of the mother cell wall before the release of the autospores (Philipose, 1967). The Lagerheimoideae are distinguished by the presence of setae, as are some members of the Tetraedronoideae.

The group which is the most difficult to distinguish from the Oocystoideae is the Ankistrodesmoideae. This group has been considered a separate family by Hindák (1970) and Fott (1971); however more recently Hindák (1977) has included the group as a sub-family within the Oocystaceae, close to the Oocystoideae. The feature that distinguishes these two groups, at whatever taxonomic level, is the lack of the expanded mother cell wall in the Ankistrodesmoideae. The autospores are released by the gelatization of the cell wall, which may produce copious mucilaginous colonies (Hindák, 1977). The identification of this group is not without problems.

The genera which have distinctly expanded and persistent mother cell walls are properly positioned within the sub-family Oocystoideae and include Oocystis and Nephrocytium. However, several other genera have not always been easily positioned and have often been referred to within the Ankistrodesmaceae, including: Kirchneriella, Nephrochlamys, Juranyiella and Podohedra (compare Korshikov, 1953; Philipose, 1967; Fott, 1971 and Hindák, 1977).

This present study will follow the arrangement of Fott (1976) for the sub-family Oocystoideae. Here Fott had made a narrower circumscription than in 1971, by leaving out Glaucocystis and most

of Kirchneriella. The genera included are Oocystis, Siderocelis, Oocystidium, Selenoderma, Neglectella, Nephrochlamys and Nephrocytium. Siderocelis and Neglectella are given as synonymous with Oocystis p.p.; whereas Selenoderma and Nephrocholamys are synonymous with Kirchneriella p.p. (Korshikov, 1953; Fott, 1976).

Hindák (1977) has erected two new genera: Granulocystis and Granulocystopsis for the species of Siderocelis which have expanded mother cell walls. He thus removed from the genus the three species Fott (1976) had combined, and restricted the definition of the genus. As a consequence, Siderocelis sensu Hindák should no longer be included in the Oocystoideae, but within the Chlorelloideae as in Korshikov (1953), because the diagnostic feature of the sub-family is the expansion of the mother cell wall around the autospores before release.

These genera have few localized species, and are largely irrelevant in the following work because they are not present in Lake Ellesmere.

The genera recorded for New Zealand are Oocystis, Nephrocytium and Granulocystis.

Genus: Oocystis A. Braun

Oocystis has been the subject of intense study in the last few years. Reháková (1969) monographed the genus for Czechoslovakia, showing the variability of the species, and detailing the extensive synonymy. This will be regarded as the basis for the current circumscription. However since this work, Fott (1976) and Hindák (1977) have removed various sections of the genus to other genera: Siderocelis Fott 1934, Neglectella Vodenicarov and Benderliev 1971 (Fott, 1976); Granulocystis Hindák 1977.

Oocystis has oval to ellipsoidal cells, which may have thickenings at the ends of the cells, or papilla. The cell walls are smooth (compare the genera Siderocelis, Amphikrikos, Granulocystis and Granulocystopsis), and enlarge after the formation of autospores. The chloroplast(s) are parietal and discoid, each with a pyrenoid (Reháková, 1969; Fott, 1976).

Reháková (1969) and Fott (1976) both point to the morphological variability within the Oocystis species. They emphasised the need for field observations to be compared with cultured material. This has led

to the reduction of distinguishable species. Brunnthaler (1915) included twenty-seven species for part of Europe, and Philipose (1967) included over forty valid names, but Fott only recognised thirteen.

Several species, following the synonymy of Reháková (1969) and Fott (1976), have been recorded for New Zealand. They include:

Oocystis borgei Snow, by Flint (1938) for Lake Sarah.

Oocystis elliptica West, by Mather, in Chapman et al. (1957).

Oocystis lacustris Chodat, by Thomasson (1960),

= ? Oocystis submarina Lagerheim, by Thomasson (1974).

Oocystis marssonii Lemm., by Flint, in Hughes et al. (1974) for Lake Ellesmere as "O. marsonii").

Oocystis naegelii A. Braun, by Nordstedt (1888).

This species is of doubtful existence (Reháková, 1969). It is based on an unpublished or unknown work by Nägeli, included by Braun when he established the genus. Type material is lacking, and the conception by several authors is completely unclear.

Oocystis parva W. and G.S. West, by Thompson in Chapman et al. (1957) (as "O. parva (Ward) G.S. West"); and Flint, in Hughes et al. (1974) for Lake Ellesmere.

Oocystis pusilla Hansgirg, by Cassie (1969) for Lake Ohakuri.

Reháková (1969) questioned the validity of this species, since the only difference from O. marssonii was ecological. Several authors have incorrectly included planktonic algae under O. pusilla (Reháková, 1969 p.172).

Oocystis solitaria Wittr. var. solitaria Wittr.

= O. solitaria var. apiculata Printz by Flint (1938) for Lake Sarah.

Granulocystis verrucosa (Roll) Hindák 1977

= Oocystis verrucosa Roll, by Flint, in Burns and Mitchell (1974) for Lake Hayes.

Three species are included in this present study for Lake Ellesmere: O. marssonii, O. parva and O. lacustris. Two other entities were noticed as transients in cultures after 5-7 weeks. They fit closely to O. pyriformis and O. borgei. It was not possible to isolate them, nor were they seen in field material.

Oocystis marssonii Lemmermann 1898c:151

(Korshikov 1953:275; Javornický and Reháková 1964:110; Reháková 1969:160; Fott 1976:195)

Cells either solitary or in colonies, in outline elliptical to flattened elliptical, sometimes also asymmetrical, with rounded or acuminated poles; average size 9.6 - 16 by 6.4 - 1.2 µm; cell membrane smooth, thin, sometimes with apical thickening. Chromatophores, each with a pyrenoid: in the autospores 1-2; the vegetative cells resulting from division, 2-4-8. Colonies either simple (from 2-4-8 cells) or rarely complex until the second generation (in older cultures until the third). Mother membrane of the younger colonies tight appressed or expanded. The daughter cells grow until the mother membrane breaks (without gelatinization). The autospores or vegetative cells are with 2 or more free chromatophores (translated from Reháková, 1969:161).

This species is distinguished from Oocystis lacustris and O. parva by the larger cells and by the number of chromatophores at the time of liberation of the autospores; and further distinguished from O. lacustris by the manner of liberation of the autospores and the character of the colony (Reháková, 1969; Fott, 1976).

Oocystis marssonii is common in freshwater, often associated with other species (Reháková, 1969). The distribution includes Europe (Reháková, 1969); USSR (Korshikov, 1953); Scandanavia (Skuja, 1964); and New Zealand (Flint, in Hughes et al., 1974).

The material from Lake Ellesmere was not as common as the other two species (Fig. 5/5 D). It was possible to distinguish this species because of two chromatophores within the autospores. The autospores were ellipsoidal 7-8 µm by 5 µm, and the vegetative cells 12-15 µm by 8-10 µm. The colonies were about 28 µm, with distinct apiculate polar thickening.

Oocystis lacustris Chodat

(Brunnthaler 1915:125; Smith 1920:112 (cells larger); Korshikov 1953:275; Prescott 1962:245 (cells larger); Javonický and Reháková 1964:110; Philipose 1967:181 (cells larger); Reháková 1969:157; Fott 1976:195)

Cells either solitary or colonial; in outline narrow to flattened elliptical, sometimes also slightly asymmetrical (L/B = 1.1-3),

with rounded or acuminated poles; extreme size 4.8-14.4 µm by 1.6-8 µm; average size 6.4-11.2 µm by 3.2-6.4 µm; mean size 8.77 ± 3.001 µm by 5.25 ± 3.00 µm. Cell membrane smooth, thin, sometimes with apical thickening, often with one layer of mucilage. Chromatophore of the autospore and the young vegetative cells is single, with one parietal pyrenoid, platelike, and is semi-circular in cross-section, with its margin either entire or lobed. Autospore formation is by division into two by older vegetative cells, chromatophores 2-4 (-8), each with a pyrenoid. Apical vacuoles with refractive particles are often found in the cytoplasm. Colonies either simple (from 2-4-8 cells) or complex (from 4-24 cells), up to three generations. The mother membrane is tightly appressed in young colonies, expanded in older, often laminated, extended through excretion of mucilage through the daughter cells. The daughter cells grow through the obstructing mucilage of the mother membrane as autospores or vegetative cells with one free chromatophore (translated from Reháková, 1969).

Oocystis lacustris is distinguished from O. marssonii by the number of chromatophores when the autospores are released, and from O. marssonii and O. parva by the manner in which the spores are released from the mother cell wall and the formation of a mucilaginous layer (Reháková, 1969; Fott, 1976).

The distribution of this species is very wide, including Europe (Reháková, 1969); Scandanavia (Skuja, 1964); USSR (Korshikov, 1953); North America (Smith, 1920; Prescott, 1962); India (Philipose, 1967; Hortobágyi, 1969) and New Zealand (Thomasson, 1960).

The material from Lake Ellesmere was larger than the mean size given by Reháková (1969). The cells were ellipsoidal, often with a wide mucilaginous layer up to 3 µm thick; cells ranged 5-12 3-9 µm (fig. 5/5c). It was found in samples throughout the collection period.

This was a new record for Lake Ellesmere.

Oocystis parva W. et G.S. West

(Smith 1920:112; Korshikov 1953:275; Prescott 1962:246; Javornický and Reháková 1969:159; Fott 1976:195)

Cells either solitary or colonial, in outline narrow to flattened elliptical, sometimes also slightly asymmetrical, with rounded or acuminate poles. Extreme size 3.2-11.2 µm by 1.6-6.4 µm;

average size 4.8-8.0 µm by 2.4-4.0 µm; mean size 6.12 ± 3.009 µm by 2.99 ± 3.007 µm. Cell membrane smooth, thin, sometimes with apical thickening. Chromatophore of the autospore and the young vegetative cells single with one pyrenoid, parietal, platelike, in cross-section semi-circular, margin either entire or slightly lobed. Older vegetative cells, as a result of division, form autospores with 2-4 (- 8) chromatophores, each with one pyrenoid. Apical vacuoles in the cytoplasm, often with refractive particles. Colonies simple (from 2-4-8 cells), mother membrane tight appressed in young colonies, with older colonies expanded. The daughter cells grow to break the mother membrane (no gelatinization) as autospores or vegetative cells with only one chromatophore (translated from Reháková, 1969:159).

O. parva is distinguished from O. lacustris and O. marssonii by a slightly smaller cell size, and from O. lacustris in the manner of liberation of the autospores. The number of chromatophores in the daughter cells separates it further from O. marssonii. In this study it was difficult to distinguish the older vegetative cells of O. parva from the autospores of O. marssonii. As a consequence these two species were grouped together during the counting procedure (Chapter 6).

This species is very widespread and commonly found in association with O. lacustris and O. marssonii (Reháková, 1969). Distribution includes Europe (Reháková, 1969); USSR (Korshikov, 1953); North America (Prescott, 1962); India (Philipose, 1967) and New Zealand (Thompson, in Chapman et al., 1957; and Flint, in Hughes et al., 1974 for Lake Ellesmere).

The present material from Lake Ellesmere fitted within the extreme sizes given earlier (Fig. 5/5B). The cells were 7-9 µm by 5-6 µm. There was only one plastid with a large pyrenoid. Little thickening was noticeable on the small vegetative cells, but the thickening was clearly apiculate on the enlarged mother cell wall. The enlarged colony was about 11 µm by 15 µm.

Genus: Nephrocytinum Nägeli 1848: 79.

Nephrocytium is distinguished from other genera within the Oocystoideae by the shape of the vegetative cells. The cells are ovoid to reniform, frequently curved (Smith, 1920; Bourrelly, 1966), having a single plastid with a pyrenoid. As with other members of this

sub-family, the mother cell wall enlarges before the release of the autospores (Bourrelly, 1966).

Several species have been recorded for New Zealand. They include:

Nephrocytium agardhianum Nägeli, by Thompson, in Chapman et al. (1957); Cassie (1978); and Cassie and Freeman (1980).

Nephrocytium limneticum (G.M. Smith) G.M. Smith, by Thompson, in Chapman et al. (1957);

= N. limneticum (G.M. Smith) Skuja, by Thomasson (1974).

Nephrocytium lunatum W. West, by Flint (1938, 1975).

Nephrocytium obesum W. and G.S. West, by Cassie (1978).

Flint (in Hughes et al. 1974) recorded Nephrocytium sp. for Lake Ellesmere. In this present study this has not been rediscovered or determined.

Sub-family 4: Ankistrodesmoideae

The inclusion of this sub-family within the Oocystaceae is not universally accepted. This group of organisms has been separated as a family in the past under various names, including Selenastraceae (West and Fritsch, 1927; Philipose, 1967) and Ankistrodesmaceae Korshikov, 1953; Hindák, 1970; Fott, 1971). More recently, however, they have been included within the Oocystaceae (Bourrelly, 1966), to the extent of forming a separate sub-family (Komárek, 1974a; Hindák, 1977).

The character which is used to distinguish this group from other members of the family is hardly sufficient to separate them very far from some members of the Oocystoideae. Hindák referred to the problems of this group, pointing out they were largely unresolved. Fott (1971) made a distinction based on whether the elongated cells were single or in colonies. However, the release of autospores from single cells (without the expansion of the mother cell wall) or the formation of mucilaginous colonies would imply a close likeness to the Oocystoideae. The confusion that has existed is illustrated by genera which have at various times been included within the two sub-families (see earlier). Kirchneriella is perhaps the most widespread example. This is included in the Oocystoideae (Fott, 1971) or

Ankistrodesmoideae (Korshikov, 1953; Philipose, 1967; Hindák, 1970, 1977; Komárek, 1974a). The Oocystoideae are distinguished as those chlorococcal green algae in which the mother cell wall expands before the release of the autospores but includes organisms in which the mother cell wall may gelatinize to effect this release (e.g. Oocystis lacustris). There is a fine line of distinction between those in which the mother cell wall ruptures without expanding, and those possessing colonial mucilage, in which the vegetative cells are later enclosed.

Even within the Ankistrodesmoideae, there are problems in the separation of some genera (Hindák, 1977). The delimitation of several genera is widely accepted (e.g. Ankistrodesmus, Pseudococcomyxa and Closteriopsis), whereas a few genera overlap in diacritical features. Hindák (1970, 1977) and Komárek (1974a) have endeavoured to present the characteristics of the genera in a way to avoid mutual overlap. The key characters for this sub-family include the attachment to the substrate or free floating; presence or absence of mucilage; arrangement of autospores in series or parallel, touching or not touching in the colony; presence or absence of pyrenoids. Hindák has included 11 genera within this sub-family, and it is on his key characters that the present generic distinction will be based. One genus that is noted for its absence is Selenastrum. This genus was at one time (West and Fritsch, 1927) the basionym for the family; however, with the revision of the genus Ankistrodesmus it has been shown that the only difference that existed between the two genera was the cell shape, and this was not stable in all cases (Komárková-Legnerová, 1969). Selenastrum was therefore placed in synonymy with Ankistrodesmus, the latter having priority (Korshikov, 1953; Legnerová, 1965; Komárková-Legnerová, 1969).

The sub-family Ankistrodesmoideae has been widely reported for New Zealand, and in view of the taxonomic problems and recent synonymy, it is worthwhile to look at each species recorded.

Species as recorded for New Zealand, with synonymy as given by Komárková-Legnerová (1969), unless otherwise stated:

Ankistrodesmus falcatus (Corda) Ralfs, by Maskell (1881) (as "A. falcatus Corda"); by Cassie (1974);
= Raphidium polymorphum Fresen. var. falcatum (Corda) Rabenh., by Nordstedt (1888);
= "Ankistrodesmus polymorphum Fresen var. falcatum (Corda) Rabenh.", by Thompson, in Chapman et al. (1957).

Ankistrodesmus fasiculatus (Lundb.) Kom.-Legn., by Cassie and Freeman (1980) (as "A. fasiculatus (Lundb.) Fott").

Ankistrodesmus gracilis (Reinsch) Kors., by Flint (1975); by Thomasson (1980);
= Selenastrum gracile Reinsch, by Mather, and Thompson, in Chapman et al. (1957); by Cassie (1974);
= Selenastrum westii G.M. Smith, by Mather, in Chapman et al. (1957) (as "S. westii Fritsch").

Ankistrodesmus mirabilis (W. and W.) Lemm.;
= Ankistrodesmus falcatus var. mirabilis (W. and G.S. West) G.S. West, by Flint, in Burns and Mitchell (1974);
= Ankistrodesmus falcatus var. mirabilis f. logiseta Nyg., by Thomasson (1960).
This species of uncertain position may be a species of Mororaphidium or Closterium (Komárková-Legnerová, 1969:113).

Ankistrodesmus spiralis (Turn.) Lemm., by Thomasson (1974);
= Ankistrodesmus falcatus var. spiralis (Turn.) G.S. West, by Chapman, and Sarma, in Sarma and Chapman (1975) (as "A. falcatus var. spiralis W. and W.").

Ankistrodesmus viridis (Snow) Bourr., by Thomasson (1974). Bourrelly (1972) made this combination from Fusola viridis Snow.

Closteriopsis longissima (Lemm.) Lemm., by Mather, in Chapman et al. (1957); Cassie and Freeman (1980) (as "Closteriopsis longissima Lemm").

Kirchneriella arcuata G.M. Smith, by Thomasson (1980).

Kirchneriella contorta (Schmidle) Bohlin, by Thompson, in Chapman et al. (1957).

Kirchneriella elongata G.M. Smith, by Cassie (1974).

Kirchneriella lagerheimii Teiling, by Johnstone (1972).

Kirchneriella lunaris (Kirchner) Moebius, by Flint (1938); Thompson, in Chapman et al., (1957); Thomasson (1974).

Kirchneriella lunaris var. dianae Bohlin, by Thomasson (1980).

Kirchneriella lunaris var. irregularis G.M. Smith, by Thomasson (1974).

Kirchneriella obesa (West) Schmidle, by Mather, in Chapman et al. (1957); Thomasson (1974).

Monoraphidium braunii (Näg.) Kom.-Legn.,

= Ankistrodesmus braunii (Näg.) Collins, by Thomasson (1974).

Monoraphidium contortum (Thuret) Kom.-Legn.,

= Ankistrodesmus contortus Thuret, by Thomasson (1974);

= Raphidium contortum (Thuret) Legn., by Flint (1966).

Monoraphidium dybowskii (Wolosz.) Hindák et Kom. Legn. by Thomasson (1980).

Monoraphidium griffithii (Berkel.) Kom.-Legn., by Thomasson (1980);

= Ankistrodesmus acutissimus Archer, by Maskell (1881);

= Ankistrodesmus falcatus var. acicularis (A.Br.) G.S. West, by Haughey (1968);

= Ankistrodesmus falcatus var. acicularis f. longissima Printz, by Thomasson (1974);

= Raphidium aciculare Rabenh., by Nordstedt (1888);

= "Ankistrodesmus polymorphum Fresen. var. aciculare (A.Br.) Rabenh.", by Mather in Chapman et al. (1957).

Monoraphidium irregulare (G.M. Smith) Kom.-Legn.,

= ? "Ankistrodesmus irregularis (G.M. Smith)", by Thomasson (1974). "A. irregularis" is not listed within the synonymy presented by Komárková-Legnerová (1969), and M. irregulare has Dactylococcopsis irregulare G.M. Smith as basionym.

Monoraphidium minutum (Näg.) Kom.-Legn., by Thomasson (1980);

= Ankistrodesmus convolutus var. minutus (Näg.) Rabenh., by Thomasson (1974);

= Selenastrum minutum (Nag.) Collins, by Haughey (1968).

Monoraphidium setiforme (Nyg.) Kom.-Legn.,

= Ankistrodesmus falcatus var. setiformis f. elongata Nyg., by Thomasson (1974).

Quadrigula lacustris (Chod.) G.M. Smith, by Johnstone (1972).

In this present study, only the genera Ankistrodesmus and Monoraphidium are further discussed.

Genus: Ankistrodesmus Corda

Following the revisions by Legnerová (1965) and Komárková-Legnerová (1969), Ankistrodesmus cells can be described as being in colonies, many times longer than broad, joined by the mid-region at least in one point, daughter cells arranged in fascicles with the mother cell wall, but are always joined into groups liberating as small colonies. Some species have colonial mucilage.

This genus is separated from Monoraphidium in which cells are solitary and arranged in series in the mother cell.

As shown previously, the New Zealand records have been confused. Extracting from the earlier synonymy, there are six species recorded for New Zealand: A. falcatus, A. fasciculatus, A. gracilis, A. mirabilis, A. spiralis and A. viridis.

For Lake Ellesmere, Flint (in Hughes et al., 1974) reported Ankistrodesmus spp. However, in this present study, they have not been rediscovered or determined, but Monoraphidium spp. are recognised.

Genus: Monoraphidium Komárková-Legnerová 1969:96.

This genus takes the solitary cells that are narrow or broadly fusiform, sometimes cylindrical, always several times longer than the width, tapering to the poles either pointed or rounded apices. Cells are straight or nearly straight, arcuate, twisted into spirals, sigmoid or crescent shape. The membrane is smooth, with no mucilage layer. Reproduction is by horizontal or slightly oblique walls, forming 2-16 autospores. Liberation of the autospores is by equatorial rupture or partial longitudinal rupture. Autospores are independent after liberation.

This genus was separated from Ankistrodesmus on the basis of solitary cells, without mucilage, in which the autospores are formed in series in the mother cell (Komárková-Legnerová, 1969).

The genus has about nineteen species (Hindák, 1977; Fott, 1981; Heynig and Krienitz, 1982). Seven species are recognised for New Zealand, following the synonymy given earlier: Monoraphidium braunii, M. contortum, M. dybowskii, M. griffithii, M. irregulare, M. minutum and M. setiforme. Three species are recognised for Lake Ellesmere.

Monoraphidium contortum (Thuret in Bréb.) Kom.-Legn. 1969:104

This species is characterized by thin fusiform cells, sigmoid or helically twisted. The cell sizes range 7-40 (-60) µm by 1-5.2 µm (Hindák, 1977).

It is difficult to separate clearly from the longer M. irregulare, which is often more helically twisted. However M. irregulare often has the chloroplast divided into two portions (Hindák, 1977).

The material from Lake Ellesmere was common in most collections, and isolated on agar plates. The cells were always curved, occasionally forming a helix sometimes up to 60 µm in nature (Fig. 5/6B). The chloroplast occupied most of the cell cytoplasm and was never divided into two portions. Autospore formation was most often into two in culture, sometimes up to eight.

This is a new record for Lake Ellesmere.

Monoraphidium griffithii (Berkel.) Kom.-Legn. 1969:98

Monoraphidium griffithii is the type species for the genus and is distinguished by long fusiform cells which are straight, or nearly straight. The cell sizes range 50-72 µm by 1.5-4 µm (Komárková-Legnerová, 1969) and up to 110 µm long (Hindák, 1977).

This species is recorded for the first time in Lake Ellesmere. The cells were longer in field material (up to 70 µm), and in culture ranged 22 - 54 µm. Mostly the cells were straight or with a very slight curvature. This species was less common than M. contortum, but was found throughout the study period.

Monoraphidium minutum (Näg.) Kom.-Legn. 1969:109

Monoraphidium minutum is strongly lunate, with rounded cell ends. The cell sizes are 6.3-17 µm by 2-7.2 µm (Komárková-Legnerová, 1969).

This species is easily distinguished from those of the same genus. However it may be confused with a single cell of Kirchneriella. The cells were always solitary and had very thin mucilage and were therefore considered as M. minutum.

The material from Lake Ellesmere had a large plastid occupying most of the cell (Fig. 5/6A). There was no pyrenoid present, although many grains were sometimes present. The cell sizes were 5-8 µm by 2.5-4 µm, with an index of curvature (Komárková-Legnerová, 1969:121) approx. 1.0.

This is a new record for Lake Ellesmere.

Sub-family 5: Tetraedronoideae

This sub-family of the Oocystaceae includes those genera with 3-5 sided cells, which are flat or tetrahedral. The corners of the cells have processes or papillae (Fott, 1971).

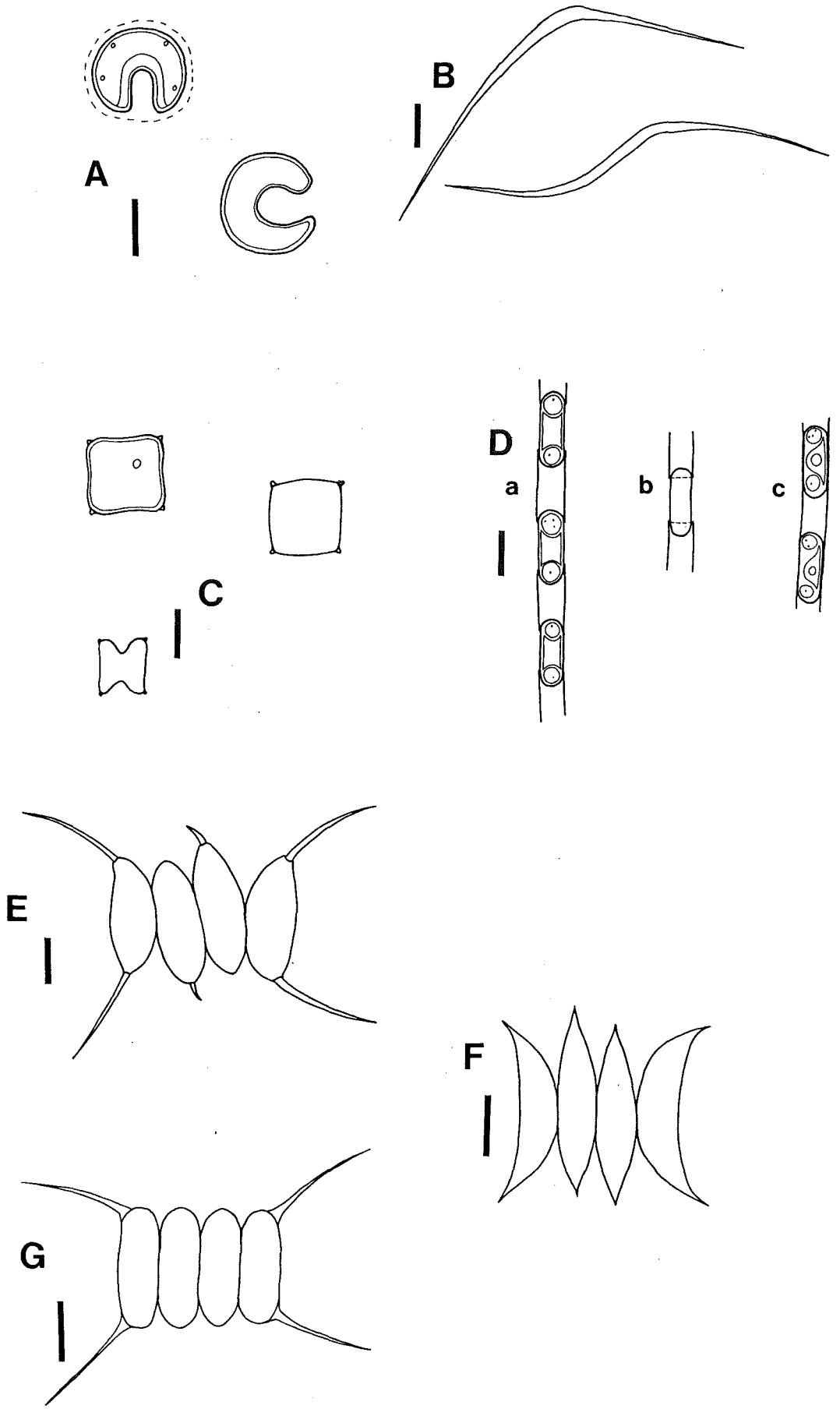


Figure 5/6: Chlorophyceae A. Monoraphidium minutum; B. Monoraphidium contortum; C. Tetraedron minimum; D. Planctonema lauterborni a-b filament form c. cell wall construction; E. Scenedesmus apoliensis; F. Scenedesmus obliquus; G. Scenedesmus quadricauda Scale 5 µm.

One genus is included in this sub-family by Fott (1971): Tetraedron; whereas other authors (Korshikov, 1953; Bourrelly, 1966) do not recognise this sub-family, but place the genus either in the Chlorelloideae or the Chlorococcaceae.

Genus: Tetraedron Kützing ex Korshikov 1953:238
nomen cons. prop. Kovácik and Komárek (1976).

Until recently this has been a widely misunderstood genus. The genus has included 95 species with 253 different taxa (Kovácik, 1975). However with the revision of the genus, and the proposal for the conservation of its name (Kovácik, 1975; Kovácik and Komárek, 1976), the genus has been reduced to about 4 species. Briefly, the taxonomic problem has involved the extension of the genus to include Polyedrium Nägeli and other genera, and the formation of combinations from genera of the Xanthophyceae and Dinophyceae. Many new species were identified, primarily by their shape, without recognition of the variability of the material. This led to an unclear, cumbersome genus (Kovácik, 1975). Korshikov (1953) reduced the genus to 6 autosporine species, and it is on this circumscription that the recent revision is based.

For New Zealand, several species of Tetraedron have been reported (Chapman et al. 1957 as "Tetraedron (Polyedrium)"; Sarma and Chapman, 1975). In view of the synonymy, as given by Kovácik (1975), it is in need of careful scrutiny. Species as recorded for New Zealand (as listed in Chapman et al., 1957; Thomasson, 1974; and Sarma and Chapman, 1975) are:

(a) Current valid species.

Tetraedron minimum (A. Br.) Hansg.

(b) Unclear, unrevised species.

Tetraedron gigas (Wittr.) Hansg.; =? Xanthophyceae

Tetraedron planctonicum G.M. Smith
= Pseudostaurastrum sp. (Xanthophyceae)

Tetraedron tetragonum (Näg.) Hansg.; unclear.

Tetraedron tumidulum (Reinsch) Hansg. = ? Xanthophyceae.

(c) Excluded species.

Tetraedron limneticum Borge;

= Pseudostaurastrum limneticum (Borge) Chodat (Xanthophyceae)

Tetraedron lobulatum (Näg) Hansg.;

= Pseudostaurastrum lobulatum (Näg) Chodat (Xanthophyceae)

Tetraedron muticum (A. Br.) Hansg.;

= Gonichloris mutica (A. Br.) Fott. (Xanthophyceae)

Tetraedron regulare Kütz.;

= Tetraedriella regularis (Kütz.) Fott (Xanthophyceae).

For Lake Ellesmere only one species is recognised:

Tetraedron minimum (A. Br.) Hansg.
(Kovácik 1975:364)

The two varieties described are separated by the nature of the cell wall, whether it is smooth or verrucose. Only the variety T. minimum var. minimum is recognised for Lake Ellesmere.

The cells are 4-cornered 8-10 µm square, about 3-4 µm thick (Fig. 5/6c). This fits well within limits given by Kovácik (1975). Each corner has a small papilla. The cell is slightly twisted so that not all the corners are in the same plane.

This is a new record for Lake Ellesmere, having been previously reported for New Zealand by Thompson (in Chapman et al., 1957) for the Rangiriri Swamp.

Family 4: Scenedesmaceae

The family Scenedesmaceae includes the green chlorococcal algae which produce coenobia (Fott, 1971; Komárek, 1974b). Reproduction usually results in multicelled coenobia by autosporulation (Bourrelly, 1966; Hindák, 1977). The diagnostic character which differentiates the Scenedesmaceae from other coenobial families is the basic number of cells, which is 4, and autosporulation. The other major coenobial family, the Hydrodictyaceae, reproduces by zoosporulation (Bourrelly, 1966; Fott, 1971).

This family is important in planktonic and soil environments, and is well represented in New Zealand, with about six genera reported (Chapman et al., 1957; Flint, 1966; Sarma and Chapman, 1975). For Lake Ellesmere, two genera have been recorded previously (Flint, in Hughes et al., 1974); but in this study only one genus has been found.

As with other chlorococcal families, there is some disagreement as to the internal classification of the family. Fott (1971) included four sub-families of different circumscription. For clarity, Fott (1971) will be followed in this treatment. Two of the sub-families are included:

1. Sub-family: Scenedesmoideae.
   Coenobia with cells in long rows, cells arranged crosswise or in a ring-shape.

2. Sub-family: Actinastroideae.
   Ceonobia with cells arranged radiately.

Sub-family 1: Scenedesmoideae

This sub-family, sensu Fott (1971), includes those coenobial forms where the cells are in long rows, arranged crosswise or in a ring-shape. Komárek (1974b) would make a narrower circumscription based on the orientation of the longitudinal axis of cells and the plane of the coenobium.

The genera included in the sub-family are: Scenedesmus, Tetrallantos, and Coronastrum. Scenedesmus is the most widespread and numerous, although one species of Tetrallantos has been recorded for New Zealand (Chapman et al., 1957). Only Scenedesmus is recorded for Lake Ellesmere.

Genus: Scenedesmus Meyen

Scenedesmus has ellipsoidal or fusiform cells grouped in a series of four or eight in a single or double row. The long axis of the cell is perpendicular to the long axis of the coenobium. The poles of the cells may be ornamented with spines, especially at the end of the coenobium. Each cell has a visible pyrenoid, and reproduces by autosporulation to form a complete coenobium (Bourrelly, 1966; Fott, 1971; Komárek, 1973, 1974b).

The genus is large, with several hundred taxa assigned to it (Bourrelly, 1966; Hindák, 1979). However, even at the generic level, there are problems in exact diagnosis. Komárek (1973) and Hindák (1979) point to the coenobial formation, presence of the pyrenoid, and the number of daughter coenobia as the generic characters.

At the infra-generic level, the taxonomy of Scenedesmus is unclear, due to the high variability of morphological features (Hindák, 1979). Two early monographs based on culture studies have been important for the development of our understanding of the genus (Smith, 1916; Chodat, 1926). The conclusions from the two monographs have led to different developments. Smith concluded that cell shape, spines, ridges and teeth were constant characters, and this led to the identification of each morphological form as a separate species or variety (Trainor et al., 1976). Many new species were described on the basis of this arrangement of ornamentation. The work of Chodat (1926), in comparison, showed that cell shape and ornamentation were not stable characters and depended on surrounding conditions. This work was largely ignored until Trainer and others confirmed the same result fifty years later (Trainor et al., 1976).

Recent work has involved electron microscope techniques to show species distinctions based on the cell formation (Komárek and Ludvík, 1973; Hindák and Klasova, 1974; Komárek et al., 1977). The usefulness of these distinctions will be in separating culture isolates and in finding constant light-microscope characteristics to differentiate the Scenedesmus taxa (Hegewald and Schnepf, 1979). This approach has not been used on sufficient taxa to enable such differentiation to be completed.

The present status of Scenedesmus is therefore unclear, but a high degree of polymorphism is accepted (Trainor et al., 1971, 1976; Hindák, 1974, 1979; Bold and Wynne, 1978) and more recent authors have erected new taxa for localized areas based on morphological characters of field material (Uherkovich, 1966; Hortobágyi, 1969).

For New Zealand, about 18 species and many varieties, have been reported (Chapman et al., 1957, Flint, 1966, 1977; Sarma and Chapman, 1975). With the present state of our knowledge it is not possible to list synonymy for these records. For Lake Ellesmere, two

species have been recorded by Flint (in Hughes et al. 1974), and in this study a further species is recorded for the first time.

Scenedesmus obliquus (Turp.) Kützing

(Brunnthaler 1915:163; Smith 1920:151; Korshikov 1953:378)

= S. acutus Meyen

(Uherkovich 1966:36)

Coenobia of (2-) 4 (-8) cells, linear or more or less alternate. Cells fusiform with acute to acuminate ends, 2.5-10 µm by 4-35 µm. Cells attached to one another for 1/3 - 1/2 their length. Outer cells may be slightly concave.

Scenedesmus obliquus is one of the spineless species of widespread distribution. It has been widely accepted as synonymous with S. acutus (Brunnthaler, 1915; Korshikov, 1953; Uherkovich, 1966), but S. obliquus has priority although it was then called Achnathes obliqua Turpin. Other species are similar including: S. acuminatus (Lagerh.) Chod. with longer acuminated cells and which may have a slightly twisted coenobium; S. dimorphus (Turp.) Kütz., which has often been included as synonymous with S. obliquus (Uherkovich, 1966); and S. acuminatus (Brunnthaler, 1915) has median cells which are more erect and terminal cells which are more convex or lunate (Smith, 1920).

The material from Lake Ellesmere was variable, showing some of the forms recognised by Uherkovich (1966; as S. acutus). The typical, most frequent coenobia had four cells, but not always in straight rows. The end cells had straight to concave outer walls; the middle cells were distinctly fusiform with acute to acuminate ends (Fig. 5/6F). Cell sizes were about medium for the referred descriptions i.e. 13-15 µm. At times the coenobia only had two cells, in which case they were most often cells of the terminal type; or coenobia may have had eight cells in two alternate series.

Scenedesmus obliquus has been recorded by Flint (in Hughes et al., 1974) for Lake Ellesmere. In the present study it was present for most of the period, except for the last autumn.

Scenedesmus quadricauda (Turp.) Bréb.

(Brunnthaler 1915:165; Smith 1920:158; Uherkovich 1966:78)

Coenobia of 2-4-8 cells, linear or more or less alternate. Cells cylindrical-ovoid with rounded or cone-shaped poles. The outer cells

are convex with a single straight or curved spine from each pole. Poles of the middle cells without spines. Cells 2.5-10 (-15) µm by (6-) 11-25 (-42) µm.

Scenedesmus quadricauda is a four-spined species which is widespread. Many infraspecific taxa have been recognised based on the size and shape of spines (Smith, 1920; Uherkovich, 1966). In view of the accepted polymorphism in it, it is not appropriate to recognise every slight variation as a separate sub-specific taxon (Trainor et al., 1971).

Other species in the sub-genus with four spines, the Quadricaudati (Uherkovich, 1966:27) include S. protuberans, S. intermedius, S. ellipsoideus, S. microspina, S. opoliensis and S. sooi. Each of these species needs to be carefully evaluated as a separate specific entity.

The material from Lake Ellesmere, previously reported by Flint (in Hughes et al., 1974), fits well within the description for the species S. quadricauda. The cells were in a linear arrangement, and their spines were only at the poles of the outer cells (Fig. 5/6G). The spines were on the whole nearly straight and fine. Cell sizes were at the small end of the range for the description; 8-10 µm by 3-4 µm.

This species was present in the lake during the early period of the study, but was largely replaced by S. opoliensis in the last autumn period. There was little confusion between these species of four-celled coenobia, although the less common two-celled coenobia were sometimes difficult to distinguish.

Scenedesmus opoliensis Richter

(Brunnthaler 1915:166; Smith 1920:159; Prescott 1962:279; Uherkovich 1966:96)

Coenobia of 2-4-8 cells in a single row. Cells fusiform or naviculoid, with the outer walls of end cells straight to convex, the lateral walls adjoined for 1/3 - 1/2 of their length. Terminal cells with long spines at each pole, central cells with or without short spines at the poles. The longitudinal axes of the central cells are not always parallel with axes of the outer cells. Cells 12-28 µm by 5-8 µm.

Scenedesmus opoliensis can be separated from S. quadricauda because of the shape of the cells, the orientation of the central cells and the presence of short spines on the central cells. Another species,

S. protuberans, appears similar, but is distinguished by Uherkovich (1966) by the shape of the apices of the cells.

This is a new record for Lake Ellesmere and fits well within the description. The cells were smaller than given, ranging 10-13 µm (Fig. 5/6 E). But with the coarse spines, both short and long, and the orientation of the cells in the four-celled coenobium, it was distinct from S. quadricauda. Only in the two-celled coenobia was there any uncertainty, but the shape of the cells (naviculoid rather than cylindrical-ovoid) allowed distinction.

S. opoliensis was found in samples over the summer and autumn of 1979-80.

Sub-family 2: Actinastroideae

Fott (1971) separates the one genus Actinastrum on the basis of having radiately arranged cells in the coenobium.

Genus: Actinastrum Lagerheim

Actinastrum hantzschii Lagerheim has been recorded for Lake Ellesmere by Flint (in Hughes et al. 1974). This has not been reconfirmed in this present study.

This species is described with truncate-fusiform cells in simple or compound colonies (coenobia), of 4 or 8 cells. The long axis of the cells radiate from a common centre. The cells are 12-22 µm by 3-5.6 µm. This is a common planktonic organism (Prescott, 1962).

5.3.2.3 Order 3. Ulotrichales

The order Ulotrichales is an assemblage of filamentous or simple green algae. The delimitation within the order has been subject to much discussion but has been partially resolved recently. Some orders of filamentous green algae are distinguished readily by vegetative and reproductive characters, such as the Oedogoniales, Conjugales and Siphonales (Ramanathan, 1964). However the classical view of the Ulotrichales distinguished no feature of reproduction by which the order might be characterized.

As a consequence of the difficulty of distinguishing special taxonomic features, there has been a proliferation of classificatory

schemes. Many of these schemes have been reviewed by Ramanathan (1964), and he showed that the delimitation of the order centred on the importance of four characters: the nature of the thallus whether simple and unbranched; the nature of the chloroplast; the reproductive bodies; and the life history. The emphasis given to each of these characters determined the breadth of the order delineation, and also the relationships of the Ulvales (-aceae), Chaetophorales (-aceae) and Oedogoniales (-aceae). The number of separate orders or the inclusion of separate families within one order ranges from one (Fott, 1971); two (Papenfuss, 1955; Printz, 1964); three (Fritsch, 1935; Smith, 1950) and more recently four (Bourrelly, 1966; Bold and Wynne, 1978).

Stewart et al. (1973) have studied the comparative cytology of many species and shown that there are major differences in mitosis, cytokinesis and the presence of plasmadesmata. Using this basis, they constructed a hypothetical classification of the green algae (Stewart and Mattox, 1975). The relevance to the present discussion is the separation of unbranched filamentous green algae into different orders and classes.

Pickett-Heaps (1975) was also of the opinion that the Ulotrichales represented a heterogeneous group. He drew the distinction between those members which contained a phycoplast and those with a phragmoplast. The phylogenic implications of this separation are important, but at the present any classification must be tentative until each genus has been investigated.

The uncertainty surrounding the order Ulotrichales and the organisms included in this present study means that further discussion at this stage is ill-advised. Only one filamentous green alga is recorded from the plankton of Lake Ellesmere: Planctonema lauterborni. Following Ramanthan (1964), the genus would be placed in the family Ulotrichaceae, close to the genera Geminella and Binuclearia, because of the form of the filament.

Family: Ulotrichaceae

Genus: Planctonema Schmidle 1903

Planctonema is a poorly known genus with one species assigned to it. It was originally placed amongst the Heterokontae (Schmidle,

1903), later considered as a doubtful member of the Heterotrichales (Pascher, 1939), and subsequently included amongst the Ulotrichales (Skuja, 1956; Bourrelly, 1966).

Within the Ulotrichales, some consider it partially synonymous with other genera. West and Fritsch (1927) include Planctonema within Geminella, whereas Printz (1927) included it within Stichococcus. Skuja (1956), on the other hand, retained the genus and considered it more closely allied to Binuclearia and Ulothrix. He also considered Planctonema as the same as his genus Psephonema from China.

Only one species is included in this present treatment.

Planctonema lauterborni Schmidle 1903
(Skuja, 1956:194)

Filament simple, free floating, almost straight or slightly bent, 2.5-4 µm wide and up to 1 mm long, without a mucilaginous sheath. Cells cylindrical, the apices rounded, 5-9-15 µm long with a relatively thin membrance. Chromatophore parietal, a simple band, nearly a completely closed cylinder or more one-sided. Pyrenoid present, although not always visible. At the ends of the cells are vacuole-like spaces which may contain small grains.

As originally described by Schmidle (1903), Planctonema lauterborni was without a mucilaginous sheath and without a pyrenoid. Schmidle's illustration (1903, Fig. 20) showed cells dispersed along the length of the filament, often in pairs, showing their origin. At the end of each cell, there was a spherical vacuole-like space, between which was a band-like chloroplast.

Skuja (1956) considered this species as the same as his Psephonema aenignaticum from China (Skuja, 1937). His description was of cylindrical cells, some with two chloroplasts, and a pyrenoid (which was not always visible). There was no mucilaginous sheath.

Bourrelly (1962) studied Planctonema lauterborni and found a thick mucilaginous sheath (up to 10 µm diameter) and no pyrenoid. Bourrelly's illustrations (1962, Fig. 36-37) show variable length cells with large single chloroplasts. The vacuole-like structures at the ends of the cells each have a single granule. In the spaces between the cells, Bourrelly has indicated cross-wall structures, unlike

Schmidle or Skuja. Some doubt may be placed upon Bourrelly's determination of the species as Planctonema lauterborni.

More recently, Akiyama and Hori (1977) looked at the fine structure of Planctonema. They found a pyrenoid, divided into two hemispheres by a simple lamella, and a matrix sheathed by two lenticular starch granules. The cell wall was composed of two elements, the individual cell envelope and the cylindrical cell wall which connected each individual cell. The connecting cell wall was the remains of the mother cell wall after division.

Planctonema lauterborni is widespread, although not common. It has been reported from Europe (Schmidle, 1903; ? Bourrelly, 1962); Scandanavia (Skuja, 1956); China (Skuja, 1937 as Psephonema aenignaticum); Japan (Haga, 1970) and New Zealand (Flint, in Hughes et al., 1974).

The material from Lake Ellesmere fitted well in the description given by Skuja (1956) (Fig. 5/6D). The filaments were without mucilage and the cells were evenly spaced, except immediately after division. Chloroplasts were most often simple bands occupying the central region of the cell, with a central pyrenoid sometimes visible. At the ends of the cells were vacuoles with enclosed grains. The cells were 6-8-(10) µm by 3-4 µm. P. lauterborni was found in all collections made throughout the sample period.

5.4 CHROMOPHYTA

The taxonomic arrangement of the Chromophyta will follow Christensen (1980).

5.4.1 Chrysophyceae and Prymnesiophyceae

Only one genus has previously been recorded for Lake Ellesmere: Ochromonas sp. (Flint, in Hughes et al., 1974). Four more genera are now reported for the first time from the Chrysophyceae and Prymnesiophyceae.

Fott (1971) distinguished the Chrysophyceae as unicellular algae with a golden or brown chloroplast. More recently, Christensen (1980) has distinguished the Prymnesiophyceae on the basis of the presence of the haptonema. This separation is also supported by others (Dodge, 1974; Bold and Wynne, 1978).

Recent reviews of these two classes are found in Pienaar (1980) and Hibberd (1980).

Class: Chrysophyceae

Order: Ochromonadales

Family: Chromulinaceae

This family is characterized as having monadoid cells, with or without bilateral symmetry. Only one flagellum projects from the cell.

Chromulina flavicans (Ehrenb.) Bütschli

(Huber-Pestalozzi, 1941: 34; Skuja, 1964:293)

Chromulina flavicans was found in a culture of lake water initiated on 6 May, 1980 (Collection 24). The live cells were 13-20 µm long, 9-12 µm wide, and of variable shape (Fig. 5/7c). One flagellum projected from the anterior end of the cell. Two peripheral chloroplasts were found in the anterior half of the cell, and one of these had a red eyespot. When the cell died it rounded and the flagellum became curled.

This species has previously been recorded for New Zealand by Thompson (in Chapman et al., 1957).

Family: Pedinellaceae

The family Pedinellaceae includes organisms with monadoid cells which are radially symmetrical about their longitudinal axis. There is frequently a circle of pseudopodia around the base of the single anterior flagellum.

Pedinella sp.

Javornický (967) considers Pseudopedinella synonymous with Pedinella and recognizes eight species within the genus, most of them from brackish water habitats.

The material from Lake Ellesmere was cultured from a sample taken on 6 May, 1980 (Collection 24). Within the cultures a range of morphological types was found and no single species description fitted the present material (Fig. 5/7A).

The smallest cells were 5.5 µm long and 4-4.5 µm wide, with an 11 µm long posterior trailing pseudopodium. A ring of these pseudopodia surrounded the single flagellum (approximately 8 µm long).

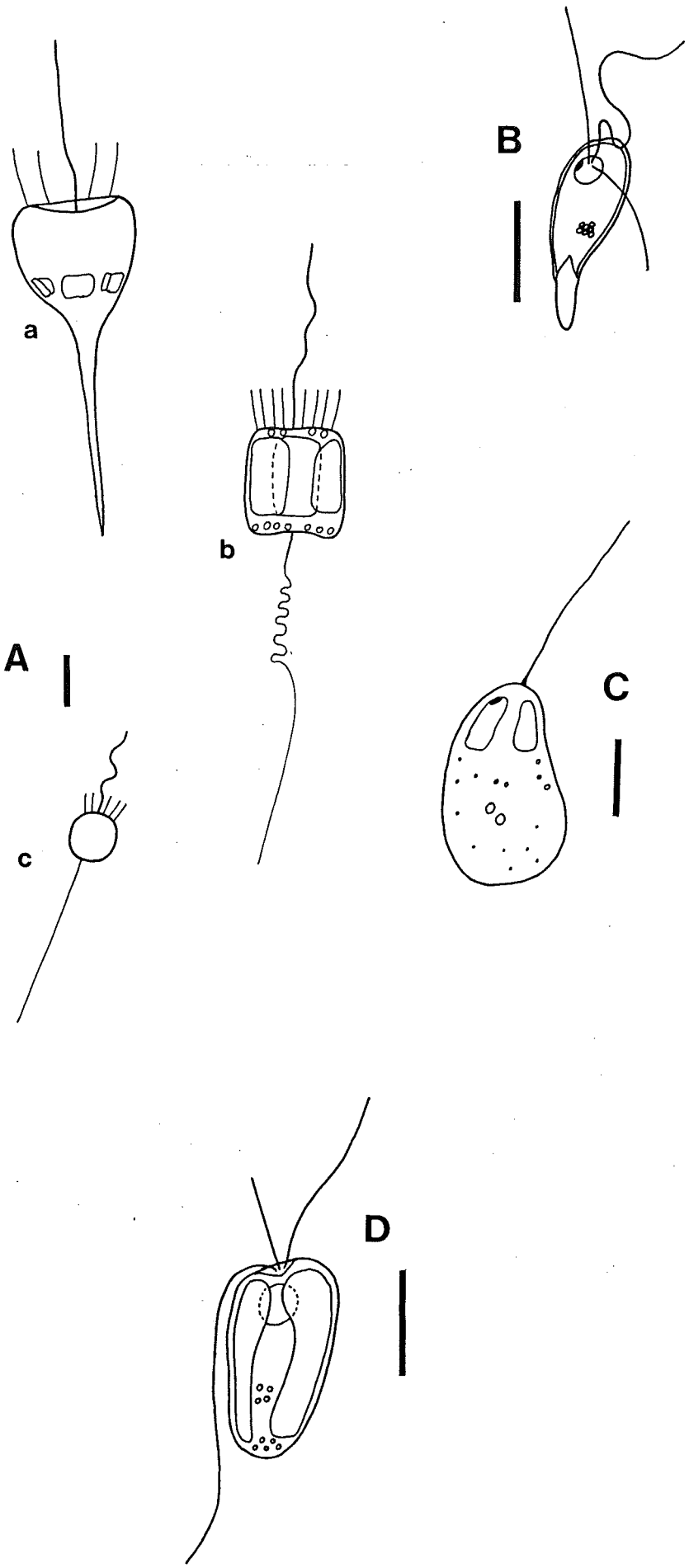


Figure 5/7: Chrysophyceae and Prymnesiophyceae
A. Pedinella sp. a-c various cell shapes;
B. Pavlova ?gyrans; C. Chromulina flavicans;
D. Prymnesium saltans.
Scale 5 µm.

No anterior invagination was observed in these small cells. The size of these cells was close to the smallest of Carter's (1937) Pseudopedinella pyriforme (= Pedinella pyriformis (Carter) Javornický), but the presence of the anterior pseudopodia does not fit her description.

Other material within the same culture was larger, and cells up to 12 µm long were found. The cells were variable in shape, some tapered toward the posterior end, but other cells did not. The posterior pseudopodium was very long, and in some cells it contracted into a coil, and propelled the cell in a new direction when rapidly uncoiled. This occurred particularly when the normal movement was obstructed. In some cells the posterior pseudopodium was much thicker and forked irregularly. In these cells no rapid movement due to coiling was observed. Most of the larger cells had a ring of anterior pseudopodia around the anterior flagellum, which arose in a small invagination. The larger cells were distinguished by the presence of only three chloroplasts, which were discoid, peripheral and ranged in size from one-third to the full length of the cell. The presence of the anterior pseudopodia suggests similarities to Pedinella elastica (Skuja) Javornický, in which the cells are larger and have six chloroplasts (Skuja, 1948). Pedinella hexocostata Vysocki and P. ambigua (Bourrelly) Javornický also have anterior pseudopodia, but the original descriptions were not available. The size of P. hexacostata as recorded by Carter (1937) is about the same as the material from Lake Ellesmere, but it has six chloroplasts.

It has not been possible to fully determine the material of Pedinella, and it may be that two separate species have occurred within this same culture.

No species of Pedinella has previously been reported for a New Zealand lake.

Class: Prymnesiophyceae (Haptophyceae)

Distinguished by the presence of an haptonoma between the two flagella.

Order: Prymnesiales

Family: Prymnesiaceae

Prymnesium saltans Massart

(Heynig, 1978)

The material of Prymnesium saltans was cultured from the same sample in which Chromulina and Pedinella were found (6 May, 1980; Collection 24). The cells were 8-12 µm long, 6-9 µm wide (mean 10.3 µm by 7.9 µm), and ovoid, with rounded or blunt apices (Fig. 5/7D). Two flagella and a short haptonoma were inserted anteriorly. One flagellum was anteriorly orientated, and the other longer flagellum trailed behind. Their two brown chloroplasts were in some cases the full length of the cell, and a vacuole was present in the anterior end of the cell. A longitudinal division from the anterior to the posterior was observed to follow the duplication of flagella, haptonema and chloroplasts. The daughter cells were mirror images of each other, rather than identical.

With its large cell size, this sample fits the recorded features of P. saltans. Other species have cells up to 10 µm long, but only up to 4.5 µm wide (Heynig, 1978). Hulbert (1965) gives cell sizes for P. parvum of 8-14 µm long, and 5-7 µm wide; these are larger then previously reported for that species, and therefore Prymnesium saltans was made a new record for Lake Ellesmere and New Zealand.

The distribution of Prymnesium saltans is not as widespread as P. parvum, which has been studied in fine-structural detail (Manton and Leedale, 1963; Manton, 1964), and ecologically (Holdway, 1978; Holdway et al., 1978). P. parvum is particularly important because of the ichthyotoxin produced in some situations (McLaughlin, 1958; Ulitzur and Shilo, 1964; Padilla et al., 1968; Shilo, 1970; Kim and Padilla, 1977; Moon and Martin, 1981).

Family: Pavlovaceae

Pavlova ? gyrans Butcher 1952.

(Green and Manton, 1970; Green, 1980)

This material from Lake Ellesmere was isolated from the same sample as the other flagellates (6 May, 1980; Collection 24). The cells were 9 µm long by 3 µm wide elongated with an obvious bulging pyrenoid at the posterior end (Fig. 5/7B). The anterior flagellum and haptonema projected forward; the trailing flagellum behind, 4.5 µm long.

Most of the cell was occupied by the chloroplast, which had a distinctive eyespot at the margin.

The description of Pavlova fits closest to that of Green and Manton (1970) for the brackish water P. gyrans. However there are some differences in that P. gyrans often has pseudopodia, and the short flagellum is usually only 3 µm long. Other similar species with the conspicuous eyespot and posteriorly bulging pyrenoid are P. granifera and P. pinguis. P. granifera is a freshwater species, and P. pinquis is marine (Green, 1980). Pavlova gyrans is the closest determination which can be made without electron microscopy data. This species is newly recorded for Lake Ellesmere and New Zealand.

5.4.2 Cryptophyceae

Only one genus has previously been recorded for Lake Ellesmere: Cryptomonas sp., by Flint (in Hughes et al., 1974). Another genus is now reported for the first time.

Gantt (1980) provides a useful review of the biology of the photosynthetic members of this class.

Order: Cryptomonadales

Family: Cryptomonadaceae

Chroomonas sp.

Chroomonas sp. was found in cultures isolated from a sample of 7 July 1980 (Collection 26). An earlier observation was made of a similar organism in August 1979.

The ovoid cells were approximately 7.5 µm long by 5 µm wide, but rounded quickly when stationary. Two flagella were inserted subapically into a furrow. These flagella were two-thirds and one-half the length of the cell respectively. Within the cell the blue-green chloroplast appeared as a peripheral lobed structure (possibly cup-shaped). A contractile vacuole was found at the anterior end and a brown eyespot was found towards the base of the flagella. Trichocysts were arranged in two longitudinal rows on either side of the flagellar invagination.

On the basis of this arrangement of trichocysts, Christensen (1980) separates Chroomonas from Cryptomonas. Both genera range in

colour from blue-green to olive-brown, and are typically planktonic in small fresh or brackish waters.

5.4.3 Dinophyceae

The Dinophyceae (dinoflagellates) form an isolated group within the Chromophyta, and are in need of taxonomic clarification (Christensen, 1980).

Order: Peridiniales

Family: Gymnodiniaceae

? Gymnodinium sp.

This organism was slightly armoured and most likely a species of Gymnodinium. The cells were more or less spherical and without spines, and were 25-35 μm in diameter. Very few cells were found throughout the two-year period, and further determination is not possible.

Flint (in Hughes et al., 1974) has previously recorded Gymnodinium sp. for Lake Ellesmere.

5.4.4 Diatomophyceae (Bacillariophyceae).

Records of over twenty diatom species from Lake Ellesmere can be found in a series of papers by Wood et al. (1959), Crosby and Wood (1959), and Wood (1961). Flint (in Hughes et al., 1974) added further records. Many of these records are of epontic species (Crosby and Wood, 1959), but they are likely to occur at times within the water column.

In the present study most diatoms were observed during the counting procedure in a preserved, uncleaned state. It has therefore been impossible to carefully determine many species, and numbers were counted according to size classes and outline shape. Biovolume calculations were based on these measurements (See Chapter 6). The full compilation of diatom species for Lake Ellesmere is given in Table 5/8. No attempt has been made to check synonymy or original descriptions of all the species listed. For the Diatomophyceae, only two new records are made for Lake Ellesmere in this present study. They are Amphiprora alata (Ehr.) Kütz. and Ditylum brightwellii (West) Grun.

5.4.5 Euglenophyceae

Fott (1971) includes the class Euglenophyceae as a group of uncertain taxonomic position. Other authors consider they form a separate division (Bold and Wynne, 1978).

For Lake Ellesmere, Flint (in Hughes et al., 1974) has recorded one genus for this class: Euglena sp. In this present study, another genus is recorded for the first time.

Class: Euglenophyceae

Order: Eutreptiales

Eutreptiella

Eutreptiella is distinguished from other genera by the presence of two emerging flagella of unequal length (Leedale, 1967). The material was found in Lake Ellesmere in a live sample collected on 9 June, 1980 (Collection 25). The cells were approximately 15-18 µm long by 8-10 µm wide. They exhibited some metaboly and at times were up to 30 µm long. Even during times of metaboly, the posterior end retained a characteristic spine-like point. The two flagella were inserted into a subapical gullet, and measured 15-18 µm and approximately 20 µm long. An eyespot was present in the anterior end of the cell near the base of the flagella. Individual chloroplasts were not distinguished although Leedale (1967) suggested that several discoid chloroplasts without pyrenoids may be present. This was not established in the case of the observed samples, nor was the presence of contractile vacuoles.

Whereas Leedale (1967) separated Eutreptiella from Eutreptia on the basis of whether the flagella are approximately equal or distinctly unequal; Bourrelly (1970) made no such distinction. Eutreptiella (sensu Leedale) includes only marine species, and Eutreptia (sensu Leedale) includes typically brackish and marine species. Whether accepted as Eutreptiella or as Eutreptia this organism is a new generic record for Lake Ellesmere. Eutreptiella marina has previously been recorded for New Zealand coastal waters by Taylor (1974).

5.5 COMPOSITION OF THE FLORA

The phytoplankton flora has been summarised in Table 5/8, where previous and new records are brought together. The total algal flora now consists of 81 entities of which one third are newly recorded in this study. It must be emphasized that the diatoms recorded are both epontic and planktonic, so this table cannot be considered a listing of only phytoplankton.

From this study 10 entities have been recorded for New Zealand for the first time. They are: Microcystis minutissima, Merismopedia tenuissima, M. punctata, Spirulina major, Oscillatoria subtilissima, Mantoniella squamata, Lobocystis sp., Pedinella sp., Prymnesium saltans and Pavlova ?gyrans. These new records represent over 12% of the lake flora, and if Ellesmere is typical of other phytoplankton-rich lakes, this highlights the general lack of knowledge of the New Zealand phytoplankton.

New taxonomic interpretations have also been given. Previously the same specific entities have been presented under different generic names; but recent revisions in taxonomic analysis have made this review imperative.

One new species has also been recognised: Lobocystis sp. nov. Although the generic placement of this species is still uncertain, it is closely allied to Lobocystis and Dichotomococcus. It has been considered preferable in the present context to record it as a manuscript description designated "sp.nov.", for future publication with Latin diagnosis and specific epithet.

From the checklist of algal species it is possible to construct a general picture of the flora of Lake Ellesmere. The three major divisions represented are the Cyanophyta, Chlorophyta and Chromophyta. Over 50% of the species are from the Chromophyta, while 12% and 35% from the other two divisions respectively. However the Chromophyta include the group of epontic diatoms. Several unknown genera were also recorded in preserved samples (see Chapter 6), so the list of flora may still be substantially increased.

New records were facilitated where organisms could be cultured, especially the Prasinophyceae, Chrysophyceae and Prymnesiophyceae. Such organisms are small and often change shape on preservation, and

Table 5/8: Algal Checklist for Lake Ellesmere.

Cyanophyta:		
Chroococcales:	Microcystis minutissima W. West	L (NR*)
	Merismopedia tenuissima Lemm.	L (NR*)
	Merismopedia punctata Meyen	L (NR*)
	Gomphosphaeria lacustris Chod.	F
	Coelosphaerium keutzingianum Naeg.	F
Oscillatoriales:	Spirulina major Kützing	L (NR*)
	Oscillatoria subtilissima Kützing	L (NR*)
	Anabaena flos-aquae Bréb.	L (NR)
	Nostoc sp.	L (NR)
	Nodularia spumigena Mert. emend. Nordin et Stein	F,L
Chlorophyta:		
Prasinophyceae		
Pyramimonadales:	Pyramimonas sp.	L (NR)
Pedinomonadales:	Nephroselmis sp.	L (NR)
	Mantoniella squamata (Manton et Parke) Desik.	L (NR*)
Chlorophyceae		
Volvocales:	Chlamydomonas sp.	F,L
Chlorococcales:	Botryococcus braunii Kützing	F,L
	Dictyosphaerium ehrenbergianum Näg.	F,L
	Dictyosphaerium pulchellum Wood	F,L
	Dictyosphaerium primarium Skuja	F,L
	Lobocystis ?sp. nov.	L (NR*)
	Chlorella vulgaris Beij.	L (NR)
	Chodatella quadriseta Lemm.	F,L
	Chodatella subsalsa (Lemm.) Lemm.	L (NR)
	Franceia ovalis (Francé) Lemm.	F,L
	Oocystis marssonii Lemm.	F,L
	O. parva W. et G.S. West	F,L
	O. lacustris Chodat	L (NR)
	Oocystis spp.	F,L
	Nephrocytium sp.	F
	Ankistrodesmus spp.	F
	Monoraphidium contortum (Thuret in Bréb.) Kom.-Legn.	L (NR)
	M. griffithii (Berkel.) Kom.-Legn.	L (NR)

Table 5/8: Continued

	M. minutum (Näg.) Kom.-Legn.	L (NR)
	Tetraedron minimum (A.Br.) Hansg.	L (NR)
	Scenedesmus obliquus (Turp.) Kütz.	F,L
	S. quadricauda (Turp.) Bréb.	F,L
	S. opoliensis Richter	L (NR)
	Actinastrum hantzschii Lager.	F
Ulotrichales:	Planctonema lauterborni Schmidle	F,L
Chromophyta:		
Chysophyceae		
Ochromonadales:	Chromulina flavicans (Ehrenb.) Bütschli	L(NR)
	Pedinella sp.	L (NR*)
	Ochromonas sp.	F
Prymnesiophyceae		
Prymnesiales:	Prymnesium saltans Massart	L (NR*)
	Pavlova ? gyrans Butcher	L (NR*)
Cryptophyceae		
Cryptomonadales:	Chroomonas sp.	L (NR)
	Cryptomonas sp.	F
Dinophyceae		
Peridiniales:	Gymnodinium sp.	F,L
Diatomophyceae:	Achnanthes coarctata (Bréb.) Grun.	W.
	A. exilis Kütz.	W
	A. hungarica Grun.	W
	A. inflata (Kütz.) Grun.	W
	A. lanceolata (Bréb.) Grun.	W
	Amphiprora alata (Ehr.) Kütz.	L (NR)
	Amphora ferroris Ehr.	W
	A. turgida Greg.	W
	Campylodiscus echeneis Ehr.	W,L
	Chaetoceros spp.	F,L
	Cocconeis placentula Ehr.	W,L
	Coscinodiscus lineatus Ehr.	WCC
	Cyclotella stelligera Cl. et Grun.	WCC, L
	Cymbella ehrenbergii Kütz.	W
	Ditylum brightwellii (West) Grun.	L (NR)
	Epithemia gibberula (Ehr.) Kütz.	W
	Hyalodiscus pustulatus A.S.	WCC, L
	Mastogloia angulata Lewis	W

Table 5/8: Continued.

	M. braunii Grun.	W
	M. cribrosa Grun.	CW
	M. pumila (Grun.) Cl.	W
	Melosira dubia Kütz.	F,L
	M. granulata (Ehr.) Ralfs	WCC, L
	Nitzschia acicularis W. Smith	F,L
	N. closterium W. Smith	F
	N. gracilis Hantz.	W
	N. sigma var. rigida Grun.	W
	Pinnularia notata Heiden et Kolbe	W
	P. viridis (Nitzsch) Ehr.	W
	Rhopalodia musculus (Kütz.) O.M.	W
	Surirella striatula Turpin	W
	Synedra tabulata (Ag.) Kütz.	W
	S. ulna (Nitzsch) Ehr.	F
Euglenophyceae:		
Eutreptiales:	Eutreptiella sp.	L (NR)
Euglenales:	Euglena sp.	F

Sources: WCC, Wood, Crosby and Cassie (1959)
CW, Crosby and Wood (1959)
W, Wood (1961)
F, Flint (in Hughes et al., 1974)
L, this study
(NR) new record for Lake Ellesmere
(NR*) new record for New Zealand

the use of liquid culture techniques (see Chapter 2.2.3) was crucial for the supply of the necessary live material for determination of the species. If the difficulties of culturing had been overcome several other species may have been identified. The new records amongst the Chlorococcales and Oscillatoriales reflect the comparative ease in culturing these organisms.

The proximity of sea water and the freshwater inflows of Lake Ellesmere largely determine the composition of its flora. The brackish quality of the water varies in different parts of the lake, and this is reflected in the sources of the recorded species. Patrick (1948) has identified groups of diatom genera associated with marine, fresh and brackish water. Hinton and Maulood (1980), Edgar (1980) and Ohtake et al. (1981) include lists of diatoms found in brackish water environments. Data on the salinity tolerance ranges of the other species is more difficult to acquire. It is possible to make an approximation from the culture media on which species have been maintained at culture centres. George (ed., 1976) and Schlösser (1982) have listed these data for the Cambridge and Göttingen collections respectively. Christensen (1980) also gives habitats at the generic level. Four groups have been identified, based primarily on generic characteristics. These groups of genera correspond primarily to marine, fresh or brackish water genera and to genera of wide ranging affinities respectively.

The first predominantly freshwater-based group includes most of the Chlorophyceae (Volvolcales, Chlorococcales, Ulotrichales), Cyclotella, Melosira, Surirella, Epithemia, Rhopalodia and Cymbella. Those mostly originating from seawater include the Prymnesiophyceae, Eutreptiella, Mantoniella, Amphiprora, Coscinodiscus and Chaetoceros. The third group of genera, those restricted to brackish water, is somewhat small in number, but does include Nodularia, Pedinella, Achnanthes, Amphora and Mastogloia.

The fourth group of genera which are widely found in both fresh and saltwater includes several of the Cyanophyta (Oscillatoria, Merismopedia, Microcystis), Prasinophyceae (Nephroselmis, Pyramimonas), Chromulina, Cocconeis, Nitzschia, Pinnularia and Synedra.

One group of phytoplankton notable for its absence is the desmids. Desmids (Chlorophyta: Conjugatophyceae, sensu Fott 1971) are exclusively

freshwater organisms (Bold and Wynne, 1978; Brook, 1981), and are often important components within oligotrophic lakes (Nygaard, 1949). Their complete absence from Lake Ellsemere indicates the fundamental importance of the brackish water for the ecology of the lake.

Nygaard's (1949) quotient hypothesis developed the compound index for phytoplankton to relate the numbers of species of certain taxonomic groups to the quality of the water. It requires the comparison of the ratio of taxonomic groups with eutrophic tendencies (Cyanophyceae, Chlorococcales, centric diatoms, englenoids) with those with oligotrophic tendencies (desmids). The quotients cannot be calculated, however, for the present study, due to the complete absence of desmids.

CHAPTER 6

PHYTOPLANKTON COMMUNITY DYNAMICS

6.1 INTRODUCTION

Phytoplankton ecology is a fast developing field, but it is one where complex issues remain unsettled. As recently as 1961 Hutchinson could describe plankton ecology as "paradoxical" because individual species coexist within the environment, while competing for similar resources. The extensive research which has developed in this field since 1961 is evidenced by the several reviews and symposia which have been published since then (Lund, 1965; Hutchinson, 1967; Round, 1971a; Owens and Esaias, 1976; Kalff and Knoechel, 1978; and Morris, ed. 1980).

Bayly and Williams (1973) considered that the factors which control phytoplankton growth were temperature, illumination and nutrient levels. These factors were described as determining the pattern of fluctuation and the seasonal succession of different species of plankton. However, as Round (1971a) pointed out, such factors as these may influence individual lakes in very different ways. Thus the present research cannot be structured around some well established model.

This chapter will analyse the fluctuations in the phytoplankton community for Lake Ellesmere during the two year period July 1978-June 1980, and attempt to relate the changes within this community to the physico-chemical environment as previously described (Chapters 3 and 4). In particular the community structure and the regulation of this structure will be highlighted. Each method of analysing the community structure has certain limitations and highlights only some factors of the lake ecology. To overcome this, the present study of community structure uses two types of data: species occurrence and species standing crop. Presence-absence data is used to illustrate the range of occurrence of each organism and thus the discussion of the composition of the flora in section 5.5 can be extended. This methodology is closely allied to that of association analysis developed by Hutchinson (1967) and as applied to New Zealand situations by Cassie (1979). Another aspect of the community structure

can be explained by resort to biovolume data. Based on the cell numbers and cell volumes of each species, the method estimates the standing crop at the time of sampling (see Chapter 2, for calculation basis). Round (1971a) considers that data based on cell volumes (here termed 'biovolume') gives a more meaningful comparison for communities which have a large number of species than does the use of cell numbers. Examples of biovolume data are given by Nalewajko (1966), Bellinger (1974), Willén (1976) and Dokulil (1979). Wu (1982) has shown the impracticability of adequate interpretation of community structures which have several taxonomic ranks. For example, the pennate diatom size class BAC6 has an uncertain specific entity, and possible inclusion of several species within its size class make ecological interpretation difficult.

As a second method, the interpretation of the phytoplankton community and its relation to the physico-chemical environment will be undertaken by multivariate statistical techniques. Because of the complexity of the physico-chemical environment and the number of species present in Lake Ellesmere a data reduction method, that of ordination analysis, is employed in this chapter.

The final aspect discussed in this present chapter is the potential limitation of the environment. Although it is not the physico-chemical parameters which are the focus of this chapter, these are the same parameters which control the phytoplankton species. Consequently this discussion is able to suggest the controls imposed upon the community, and it can recognise how changes in the environment may affect the phytoplankton.

The data base used in this chapter is restricted to the 206 samples for which phytoplankton counts were made. This is rather less samples than were available for the analysis of the physico-chemical variables ($n \leqslant 256$). Species were analysed in a preserved state and sixty-one were positively identified. Not all species could be identified from preserved samples alone (see Chapter 5), and as a consequence several species are referred to as "Unknown sp.". Table 6/1 gives the identity, name and number codes and calculated biovolume of each species considered in this chapter.

Table 6/1: Species Identification and Dimensions

Taxonomic Grp.	Species Identification	Code Name[*1]	Number[*2]	Shape[*3]	L(µm)	W(µm)	D(µm)	Volume[*4] (µm³)
1. Cyanophyta	Merismopedia tenuissima	MER1	1	SP	1.5	1.5		1.7672
	M. punctata	MER2	2	SP	3	3		14.1372
	Unknown[*6] 15	S15	3	SP	3	3		14.1372
	Microcystis minutissima	MICMIN	62	EL	1.8	1.2		1.3572
2. Chlorophyta	Monoraphidium contortum	MONSP1	4	DC	60	2		62.832
	M. minutum	MONSP2	5	DC	6.5	3		15.3153
	M. griffithii	MONSP3	6	DC	50	2		52.36
	Chlamydomonas sp.	CHLAMY	7	SP	12	12		904.78[*7]
	Chlorella vulgaris	CLOVUL	8	SP	5	5		65.45
	Chodatella quadriseta	CHO1	9	EL	10	5		130.9
	C. subsalsa	CHO2	21	EL	10	5		130.9
	Lobocystis sp. nov.	LOBO	10	EL	6	3		28.274
	Dictyosphaerium primarium	DICPRI	11	SP	2	2		4.1888
	D. pulchellum	DICPUL	12	SP	7	7		179.5948
	D. ehrenbergianum	DICEHR	13	EL	8	3.5		51.3128
	Oocystis parva, O. marssonii	OOCY	14	EL	8	5.5		126.7112
	O. lacustris	SP8	20	EL	8.5	6		160.2216
	Planctonema lauterborni	PLALAU	15	RO	7	3		49.4802
	Scenedesmus obliquus	SCEOBL	16	DC	14.5	4.5		76.8710
	S. quadricauda	SCEQUA	17	RO	9	3.5		86.590
	S. opoliensis	SCEOPOL	18	DC	11	5		71.995
	Tetraedron minimum	TETMIN	19	TE	9	9	3	243.0
	Unknown[*6] 11	S11	22	SP	15	15		1767.15
	43	S43	23	SP	10	10		523.6
	44	S44	24	EL	12	10		628.32
	47	S47	26	SP	10	10		523.6
	Crucigenia sp.	CRU	27	SP	3	3		14.1372
	Actinastrum sp.	ACT	28	RO	20	3		141.372
3. Englenophyceae	Unknown[6*] 50	S50	29	CO	8	3		18.8496
4. Chromophyta, Chrysophyceae	Unknown[6*] 21	S21	30	CO	5	5		32.725
	22	S22	31	EL	8	4		67.0208
	24	S24	32	SP	15	15		1767.15
	32	S32	33	CO	12	8		201.062[*7]
	40	S40	34	TE	10	10	10	1000.0
	42	S42	35	EL	15	6		282.744
	46	S46	36	CO	20	10		523.6
	48	S48	37	EL	15	6		282.744
	51	S51	38	DC	8	3		18.8496
	52	S52	39	SP	10	10		523.6[*7]
	53	S53	40	TE	6.5	6.5	6.5	274.625
	54	S54	41	RO	8	10		628.32
	56	S56	42	EL	15	12		1130.976
	60	S60	60	SP	5	5		65.45
	57	S57	61	SP	4	4		33.51
5. Diatomophyceae	Pennate diatoms[*5] 3	BAC3	43	TE	20	3	2	120.0
	4	BAC4	44	TE	10	2	2	40.0
	6	BAC6	45	TE	15	3	2	90.0
	7	BAC7	46	TE	100	10	2	2000.0[*7]
	8	BAC8	47	TE	10	6	2	120.0[*7]
	12	BAC12	58	TE	50	4	4	800.0
	Synedra sp.	BAC10	48	TE	45	10	3	1350.0
	Chaetoceros sp. 1	CHESP1	49	TE	10	5	2	100.0[*7]
	C. sp. 2	CHESP2	54	TE	12	8	2	192.0
	Melosira granulata	MELGRA	50	RO	20	6		545.488
	M. sp. 2	MELSP2	51	EL	12	10		628.32[*7]
	Nitzschia sp.	NIT	52	DC	90	2		94.248
	Amphiroroa sp.	AMP	53	TE	80	30	5	12000.0
	Coscinodiscus sp.	COS	55	RO	5	25		2454.375
6. Cryptophyceae	Unknown[*6] 26	S26	56	CO	50	10		1309.0
	58	S58	57	EL	8	4		67.021
7. Dinophyceae	Gymnodinium sp.	DINO	59	SP	30	30		14137.2[*7]

Footnotes:

[*1] code name designation used in Figures 6/5 to 6/13

[*2] number designation used in Figures 6/15 ABC

[*3] shape, as defined Table 2/8

[*4] volume as calculated by BIOMASS program

[*5] pennate diatoms, several species included (?), by size class

[*6] Unknown - uncertain generic determination (see Chapter 5).

[*7] sizes varied in some samples, only most frequent volume given.

6.2 COMMUNITY STRUCTURE

The phytoplankton species present in the 206 samples over the period July 1978 to July 1980 (25 collections) are shown in Table 6/2. It is evident from this table that the occurrence of species fluctuates. Some species were present in all samples while other species appeared in most samples and others occurred in very few. The only species to occur in all of the samples was Dictyosphaerium primarium, although several other green algae appeared in over 90% of samples. The most frequently occurring diatoms were the size class BAC6 (see Table 6/1 for explanation) and Chaetoceros spl, which were found in 88.8% and 84% of the samples respectively. The most common blue-green alga was Merismopedia punctata, which was found in 56.7% of the samples. No species of Chrysophyceae, Euglenophyceae, Cryptophyceae or Dinophyceae was in evidence in more than 50% of the samples.

The number of samples in which a species occurred shows a disjunct distribution (Figure 6/3B). Calculated from the occurrence of species expressed as a percentage, this disjunction is between species that occur in less than 71% of the samples (the infrequent species), and the "frequent species" found in more than 84% of the samples. No importance should be attached to the empirical percentage recorded, but this disjunction is sufficiently large to justify interpretation.

The most frequent species were found in a range from 84 to 100% of the samples; and green algae contributed most species to this group. Dictyosphaerium primarium was found in each sample, and D. pulchellum, Oocystis parva (+ O. marssonii, see Chapter 5 for explanation) and Planctonema lauterborni occurred in more than 99% of the samples. The other frequently occurring species were Monoraphidium contortum, Chodatella quadriseta, Lobocystis sp., Oocystis lacustris and Chaetoceros spl. Although BAC6 occurred in 89% of samples, it will not be discussed further because of the nonspecific nature of the size class. Among the infrequently occurring group of species, a high proportion occurred relatively rarely, with only a few occurring in anything approaching the upper figure of 71% (Figure 6/3B). Twenty species, about one third of the recorded entities, occurred in not more than 5% of the samples. A further seven entities occurred in less than 10% of the samples. These infrequent entities were generally too rare

Table 6/2: Species Present in Each Sample

Sample No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Colln. No.											3											4									5								6	
Site No.	1	2	5	6	8	10	11	12	13	14	1	2	4	5	6	8	10	11	12	13	14	1	2	4	6	8	10	11	12	14	1	2	4	5	6	10	11	14	2	4
Spp. No	Spp. Code																																							
1	MER1																													+								+	+
2	MER2	+	+									+		+				+	+	+	+																		
3	S15	+		+								+		+								+	+						+			+			+		+		+
4	MONSP1	+	+	+	+	+	+	+	+	+	+	+									+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
5	MONSP2											+										+																+		
6	MONSP3										+	+	+	+	+		+	+	+	+	+	+									+	+			+				
7	CHLAMY	+	+	+		+							+	+	+		+			+	+																		
8	CLOVUL																														+	+	+		+	+				
9	CHO1	+	+	+	+		+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+			+				+	+	+	+	+	+	+	+	+	+
21	CHO2	+	+	+	+		+		+	+	+	+	+	+					+	+	+	+	+	+	+						+	+	+		+	+		+		
10	LOBO	+	+	+	+		+	+	+	+	+	+	+	+	+			+	+	+	+	+										+	+	+	+	+	+	+	+	+
11	DICPR1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12	DICPUL	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
13	DICEHR																														+	+			+	+	+		+	+
14	OOCY	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	PLALAU	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	SCEOBL									+											+	+									+		+	+	+		+	+		
17	SCEQUA	+		+			+	+			+	+	+		+	+		+	+	+	+	+				+		+			+		+		+		+	+	+	+
18	SCEOPOL																																							
19	TETMIN	+	+	+	+		+	+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+			+		+		+	+	+	+	+	+	+	+	+
20	SP8	+	+	+			+	+	+	+	+	+	+	+	+		+		+	+	+	+	+					+	+	+			+	+		+		+		+
22	S11	+	+	+						+		+								+	+	+																		
23	S43	+		+				+	+		+	+		+			+		+	+	+		+				+									+	+	+		+	+
24	S44																																							
26	S47																																							
27	CRU																																							
28	ACT																																							
29	S50	+					+	+	+	+		+		+	+	+				+	+	+		+																
30	S21																																+	+							+
31	S22													+																											
32	S24		+											+	+	+							+							+											
33	S32																		+																					
34	S40																							+	+					+						+				
35	S42																																			+		+	+		
36	S46																																							
37	S48																																							
38	S51																																							
39	S52																																							
40	S53																																							
41	S54																																							
42	S56																																							
43	BAC3	+	+	+			+				+		+	+				+	+		+	+		+			+			+			+	+	+			+	+
44	BAC4	+	+	+																																	+				
45	BAC6	+	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
46	BAC7	+		+						+												+								+										
47	BAC8	+	+	+																																					
48	BAC10	+																								+															
49	CHESP1	+	+	+			+	+	+	+	+	+			+	+		+	+	+	+	+	+	+							+	+			+	+	+	+	+	+
50	MELGRA	+	+					+			+	+		+	+		+		+				+																	
51	MELSP2													+								+	+			+				+						+	+			+	+
52	NIT	+		+			+	+	+	+		+							+	+		+	+	+															+	+
53	AMP																																							
54	CHESP2																				+																			
55	COS																																							
56	S26												+																											
57	S58																																							
58	BAC12																																							
59	DINO																																							
60	S60																																							
61	S57																																							
62	MICMIN																																							
Total		26	20	22	10	4	17	15	16	16	15	19	15	17	22	13	7	15	17	17	22	25	16	17	11	6	9	11	7	10	10	18	15	16	14	20	15	16	15	19	20

Table continued over. A one-page copy of this table is given as Supplementary Table 3.

Table 6/2 continued.

Sample No.	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Colln. No.									7			8							9											10							11			
Site No.	5	6	8	10	11	12	13	14	2	5	14	6	8	10	11	12	13	14	1	2	4	5	6	8	10	11	12	13	14	1	2	5	6	10	12	13	14	1	2	4
Spp. No	Spp. Code																																							
1	MER1	+	+							+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	
2	MER2					+	+		+			+	+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	
3	S15								+																															
4	MONSP1	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
5	MONSP2	+		+		+	+					+									+		+	+	+			+	+	+	+				+	+	+			
6	MONSP3																			+			+	+								+					+	+			
7	CHLAMY																	+						+	+		+		+											+
8	CLOVUL	+																				+												+	+						
9	CHO1	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
21	CHO2	+		+	+	+				+	+															+	+	+													
10	LOBO	+	+	+	+	+	+	+	+	+	+			+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11	DICPR1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12	DICPUL	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
13	DICEHR	+	+	+		+	+	+	+		+	+		+	+			+	+		+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+
14	OOCY	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	PLALAU	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	SCEOBL	+	+	+	+	+	+			+	+		+		+			+	+	+	+	+	+	+	+		+	+	+	+	+			+	+		+			
17	SCEQUA	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
18	SCEOPOL																																							
19	TETMIN	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+		+	+	+	+
20	SP8	+	+	+	+					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+				+	+		+	+		
22	S11																																							
23	S43				+	+	+									+									+															
24	S44						+																				+													
26	S47																		+							+													
27	CRU																																		+	+				
28	ACT																																							
29	S50																																							
30	S21			+															+		+	+	+		+															
31	S22																																							
32	S24																																							
33	S32													+	+												+													
34	S40																							+																
35	S42																								+		+	+												
36	S46																																							
37	S48																																						+	
38	S51																																							
39	S52																																							
40	S53																																							
41	S54																																							
42	S56																																							
43	BAC3		+	+	+		+		+				+					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+		
44	BAC4																																							
45	BAC6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+
46	BAC7			+		+	+	+										+																					
47	BAC8												+						+	+		+	+			+		+	+	+	+		+		+	+			+	
48	BAC10																																							
49	CHESP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+		+	+	+	+	+		+	+	+		+	+	+
50	MELGRA								+										+						+															
51	MELSP2		+				+	+	+				+	+		+		+	+		+	+					+	+	+	+	+		+	+				+		+
52	NIT	+		+	+	+	+	+	+	+			+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+		
53	AMP																						+				+													
54	CHESP2																																							
55	COS																																			+				
56	S26																																							
57	S58																																							
58	BAC12																																							
59	DINO																																							
60	S60																																							
61	S57																																							
62	MICMIN																																						+	
Total		19	17	18	17	19	21	17	18	11	15	18	15	16	15	15	12	19	21	22	19	21	23	23	23	22	20	23	23	21	20	18	19	12	15	21	20	17	19	18	14

Table 6/2 continued.

Sample No.		81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Colln. No.								12	13											14											15			16								
Site No.		5	6	8	10	11	12	4	1	2	4	5	6	8	10	11	12	13	14	1	2	4	5	6	8	10	11	12	13	14	1	2	11	1	2	4	5	6	8	10	11
Spp. No.	Spp. Code																																								
1	MER1																																								
2	MER2	+	+		+		+	+		+					+			+		+	+				+			+							+					
3	S15														+																										
4	MONSP1	+	+	+	+	+	+		+	+		+	+	+	+			+	+	+	+		+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+
5	MONSP2	+	+					+																						+											
6	MONSP3		+		+	+		+	+	+	+		+	+	+	+		+	+	+	+	+	+	+	+		+	+	+	+	+		+	+	+	+	+	+	+	+	
7	CHLAMY				+				+	+			+				+	+	+	+	+																+					
8	CLOVUL								+	+		+		+	+	+	+	+	+	+	+	+	+	+	+		+			+												
9	CHO1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
21	CHO2																																								+
10	LOBO	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11	DICPR1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12	DICPUL	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+			+	+
13	DICEHR	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+	+	+	+			+	+	+	+		+		+	+		+	+	+	+	+	+
14	OOCY	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	PLALAU	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	SCEOBL	+	+		+	+		+	+											+	+	+					+	+	+		+		+	+	+	+	+	+	+	+	+
17	SCEQUA	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
18	SCEOPOL												+																				+								
19	TETMIN	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+				+		+		+	+	+		+		+	+	+		+	+	+	+
20	SP8	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+			+	+	+	+	+		+	+	+	+	+	+	+	+	+	+
22	S11																																								
23	S43								+	+	+	+			+			+		+		+		+					+	+		+	+	+	+	+	+	+	+	+	+
24	S44																																								
26	S47																																								
27	CRU																																								
28	ACT								+																																
29	S50		+	+	+				+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+				+				
30	S21																																								
31	S22		+																																						
32	S24																																								
33	S32																			+	+	+	+		+	+	+				+	+	+	+	+	+	+	+	+	+	+
34	S40																																								
35	S42																																								
36	S46																									+		+						+							
37	S48												+						+																							
38	S51			+					+											+	+	+			+	+	+	+	+			+	+			+		+			
39	S52								+	+	+		+	+						+	+																					
40	S53									+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+	+		+			+	+	+			+		
41	S54																+	+	+		+	+	+		+	+	+	+	+	+	+	+	+				+				+	
42	S56																			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
43	BAC3	+	+	+	+		+		+	,		+		+						+	+	+	+			+	+	+	+												
44	BAC4																																								
45	BAC6	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+		+	+		+						
46	BAC7																																								
47	BAC8	+																																							
48	BAC10									+																															
49	CHESP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
50	MELGRA												+																												
51	MELSP2			+		+	+						+																			+				+				
52	NIT		+	+	+	+		+	+		+						+																							
53	AMP																															+									
54	CHESP2																																								
55	COS																																								
56	S26																					+																			
57	S58																					+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
58	BAC12																																								
59	DINO																																		+				+		
60	S60																			+		+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
61	S57																																								
62	MICMIN	+		+	+	+				+	+	+	+	+	+				+		+																			
Total		19	20	18	22	17	16	24	24	17	20	23	20	21	17	16	19	21	26	24	24	22	14	13	26	22	24	23	21	16	24	22	22	22	19	24	20	20	21	19	

Table 6/2 continued.

Sample No.	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Colln. No.				17			18										19				20									
Site No.	12	13	14	1	2	11	1	2	4	5	6	8	10	11	12	13	14	1	2	11	1	2	4	5	6	8	10	11	12	13
Spp. No	Spp. Code																													
1	MER1						+		+		+	+					+	+	+	+	+	+	+	+	+	+	+	+	+	
2	MER2				+	+		+	+		+		+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	
3	S15																	+	+											
4	MONSP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
5	MONSP2		+				+	+	+	+	+				+	+	+	+		+	+	+	+	+	+	+	+	+	+	+
6	MONSP3	+	+	+	+	+	+	+	+		+				+		+				+	+	+		+	+	+			
7	CHLAMY																+		+									+	+	
8	CLOVUL																													
9	CHO1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
21	CHO2			+	+		+	+	+		+	+		+	+	+	+	+		+	+	+						+	
10	LOBO	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		
11	DICPR1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12	DICPUL	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
13	DICEHR	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
14	OOCY	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	PLALAU	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	
16	SCEOBL	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
17	SCEQUA	+	+	+	+	+	+	+	+		+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
18	SCEOPOL							+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
19	TETMIN							+	+		+	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	
20	SP8	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
22	S11																													
23	S43	+	+	+					+		+																			
24	S44																													
26	S47																													
27	CRU																													
28	ACT																													
29	S50						+																							
30	S21																													
31	S22																													
32	S24																													
33	S32	+		+	+	+	+			+	+							+		+		+								
34	S40																													
35	S42																													
36	S46			+																										
37	S48																													
38	S51					+	+													+										
39	S52																		+							+				
40	S53	+		+																										
41	S54					+																								
42	S56	+		+			+																	+						
43	BAC3																													
44	BAC4																													
45	BAC6			+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
46	BAC7																													
47	BAC8				+														+											
48	BAC10																													
49	CHESP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+											+
50	MELGRA				+																									
51	MELSP2							+		+				+				+		+		+	+				+			
52	NIT							+										+	+	+	+		+	+			+	+	+	
53	AMP																													
54	CHESP2		+											+																
55	COS																													
56	S26																													
57	S58	+	+	+	+	+	+		+						+															
58	BAC12																													
59	DINO				+		+	+	+						+		+									+			
60	S60																													
61	S57	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
62	MICMIN																	+	+	+	+	+	+	+	+	+	+	+	+	
Total	19	17	22	21	20	23	21	24	19	20	21	17	17	17	20	19	22	24	24	24	22	23	23	20	20	22	22	19	22	6

Table 6/2 continued.

Sample No.	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Colln. No.		21								22								23										24		
Site No.	14	4	6	8	10	11	12	13	14	1	2	4	5	6	8	10	13	1	2	4	5	6	8	10	11	12	14	1	2	4
Spp. No	Spp. Code																													
1	MER1	+		+	+	+	+			+																				
2	MER2	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3	S15				+	+												+	+		+		+		+	+	+			
4	MONSP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
5	MONSP2	+	+	+	+	+	+	+			+		+	+			+	+		+	+		+	+	+	+	+		+	+	+
6	MONSP3		+	+		+	+	+		+	+			+				+				+								+	
7	CHLAMY																														
8	CLOVUL																														
9	CHO1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
21	CHO2																											+	+	+	+
10	LOBO	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11	DICPR1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12	DICPUL	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
13	DICEHR	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+			
14	OOCY	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	PLALAU	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	SCEOBL	+	+	+																											
17	SCEQUA	+									+																				
18	SCEOPOL	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+			+		+	
19	TETMIN	+		+	+	+	+	+	+	+	+	+	+		+							+	+	+			+				+
20	SP8	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
22	S11																														
23	S43																														
24	S44																														
26	S47																														
27	CRU																														
28	ACT																														
29	S50																														
30	S21																														
31	S22																														
32	S24																														
33	S32							+				+	+										+								
34	S40																														
35	S42																														
36	S46																														
37	S48																														
38	S51							+																							
39	S52		+																												
40	S53																														
41	S54																														
42	S56																														
43	BAC3	+																		+				+	+	+					
44	BAC4																														
45	BAC6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
46	BAC7																		+		+		+	+	+		+	+			
47	BAC8	+																													
48	BAC10																														
49	CHESP1		+	+	+	+	+	+	+		+	+	+	+	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+
50	MELGRA								+																						
51	MELSP2		+	+	+	+	+	+	+		+		+	+	+	+	+		+	+	+	+	+	+	+	+	+		+		
52	NIT	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+
53	AMP																														
54	CHESP2																														
55	COS	+																													
56	S26																														
57	S58										+								+	+	+	+	+	+	+	+	+	+		+	
58	BAC12							+			+	+	+																		
59	DINO					+		+																							
60	S60																														
61	S57	+	+		+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
62	MICMIN	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Total		23	20	21	20	23	19	23	19	18	22	20	20	20	17	18	17	20	19	20	20	20	22	22	22	19	20	20	18	19	18

Table 6/2 continued.

Sample No.	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	
Colln. No.								25									26										
Site No.	5	6	8	10	12	13	14	1	2	4	5	6	8	10	11	13	1	2	4	6	8	10	11	12	13	14	
Spp. No	Spp. Code																										Total
1	MER1																										55
2	MER2		+	+		+	+	+		+	+	+	+		+	+	+	+	+	+		+		+	+	+	+	117
3	S15	+			+	+																					27
4	MONSP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	186
5	MONSP2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	93
6	MONSP3																	+										80
7	CHLAMY														+			+	+	+	+		+				+	36
8	CLOVUL																											27
9	CHO1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	192
21	CHO2		+	+	+	+	+	+																				62
10	LOBO	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	184
11	DICPR1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	206
12	DICPUL	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	201
13	DICEHR		+	+	+				+		+	+			+							+	+	+				139
14	OOCY	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	205
15	PLALAU	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	204
16	SCEOBL																											90
17	SCEQUA																											128
18	SCEOPOL			+				+	+	+					+	+			+						+			57
19	TETMIN				+	+				+	+		+				+				+				+		+		146
20	SP8		+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	175
22	S11																											8
23	S43																											49
24	S44																											2
26	S47																											2
27	CRU																											1
28	ACT																											1
29	S50																											42
30	S21																											9
31	S22																											2
32	S24																											6
33	S32	+	+		+	+																						40
34	S40																											4
35	S42																											3
36	S46																											7
37	S48																											3
38	S51																											18
39	S52																											10
40	S53																											25
41	S54																											18
42	S56																											25
43	BAC3											+		+														68
44	BAC4																											4
45	BAC6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+	+		+	+	183
46	BAC7							+		+																		19
47	BAC8																											20
48	BAC10																											3
49	CHESP1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	173
50	MELGRA																											16
51	MELSP2					+	+		+						+													72
52	NIT	+		+				+			+			+			+		+		+	+		+	+	+		105
53	AMP																											3
54	CHESP2																											3
55	COS																											2
56	S26																											2
57	S58	+	+		+	+			+	+	+	+	+	+	+				+	+	+	+			+			58
58	BAC12																											4
59	DINO																											11
60	S60																+	+	+	+	+	+	+	+	+	+	+	11
61	S57	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	101
62	MICMIN	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	81
Total		16	18	17	20	19	16	17	17	19	17	17	18	14	18	19	14	18	18	17	17	17	17	17	18	17	17	

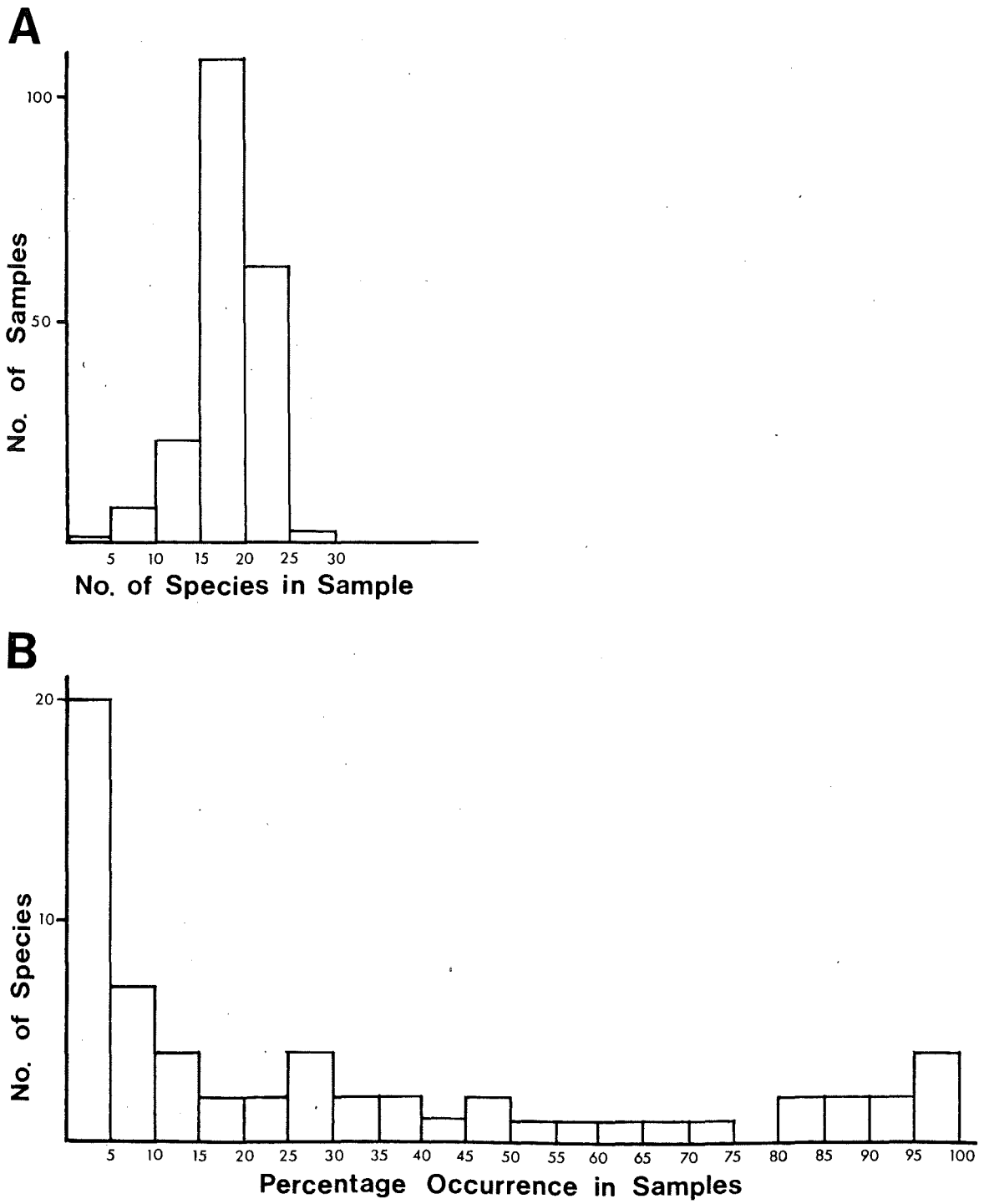


Figure 6/3: A. Frequency Distribution of Number of Species in each Sample.
B. Frequency Distribution of Percentage Occurrence of Samples in which the Species were Present.

to enable adequate identification, so they have only been distinguished with respect to their cell shape and size. Within this category, there were five unidentified green algae (Crucigenia sp., Actinastrum sp., and Unknown spp. S11, S44 and S47), most of the Chrysophyceae, several Diatomophyceae, Cryptophyceae and the Dinophyceae. The taxonomically uncertain species must, as has already been said, be treated with caution because of the possibility of grouping several separate 'species' into one coded entity.

The total number of species present in each sample is also shown in Table 6/2. The mean number of species present in the samples was 18.7, ranging from four to twenty-six. Over half of the samples (n = 206) had 16 to 20 species present, and 94% had between 11 and 25 species. Lilliefors Test (Conover, 1980) was used to check this frequency distribution (Figure 6/3A) of the number of species within each sample (see section 2.3, for explanation of this test). The calculated test statistic, D, was 0.1139, using the K-S (NORMAL) option of the NPAR TESTS subprogram (SPSS, 1981). The critical value, T, for Lilliefors Test (n = 206) at the 95% confidence level was 0.0617, therefore this data does not have a normal distribution. However there is an evident central tendency within the frequency distribution as illustrated in the figure.

The samples with the least number of species present were commonly collected at sites near the inflows and the outflow. Low numbers of species were recorded at Site 8, off the Selwyn River, on occasions when the inflow rate was high. High inflow thus diluted the lake biota, rather than augmenting the population of phytoplankton species. At site 13, close to Taumutu, a mere six species were counted in Collection 20 (11 December, 1979), and each was a "frequent" species. The high seawater inflow into the lake about this time is no doubt reflected in this result.

Table 6/2 also indicates the changing patterns of the occurrence of species during the passage of time. In this table the content of the samples is displayed in chronological order of collection. It is apparent that the occurrence of some species goes in phases. Thus many of the Chrysophyceae appeared between Collection 12 (May 1979) and Collection 17 (October 1979). At the same time fewer diatom species occurred in the counts.

Other species which appeared concentrated in a short time-span included Chlorella vulgaris, Chodatella subsalsa, Unknown spp. S43, S50 and S57.

Microcystis minutissima, which appeared at a few sites late in the summer of 1979, did not appear in any samples at all from August to November later in the same year, but during the summer of 1980 it became a dominant species throughout the lake (see section 6.3.1).

6.3 PHYTOPLANKTON STANDING CROP

The phytoplankton standing crop is measured in two ways in this present study; by way of cell numbers and 'biovolume' (calculated from cell numbers and cell volumes).

Figure 6/4A shows the log plot of total cell numbers, based on the mean number on each collection date. A seasonal cycle is evident with summer levels higher than winter levels. The occurrence of these peak levels is not precisely determined seasonally, however, so other changeable factors within the lake system must also be involved. The mean number of cells in the lake was at its height in May 1980, at 4.7×10^6 cells per ml, and one site (site 14) reached a peak of 5.9×10^6 cells per ml.

In this study greater emphasis is placed on the biovolume of phytoplankton than on cell numbers. This is a more meaningful representation of the community than cell numbers because of the variation in specific cell sizes.

Table 6/1, already referred to (see section 6.1) shows the range of cell volumes of individual species from 1.35 μm^3 for Microcystis minutissima to 14137.2 μm^3 for Gymnodinium sp. When the cell numbers are incorporated to express total biovolume of these organisms the large Gymnodinium, despite the large volume of each cell, was a small part of the total standing crop at any one time.

Figure 6/4B shows the total biovolume for the lake on a time scale. The seasonal fluctuation is again evident, with the level in late summer and autumn 1980 particularly high. The maximum mean biovolume was in February 1980 at 31.08 $cm^3.m^{-3}$, and the maximum for a single site was 35.95 $cm^3.m^{-3}$. The lowest mean biovolume was

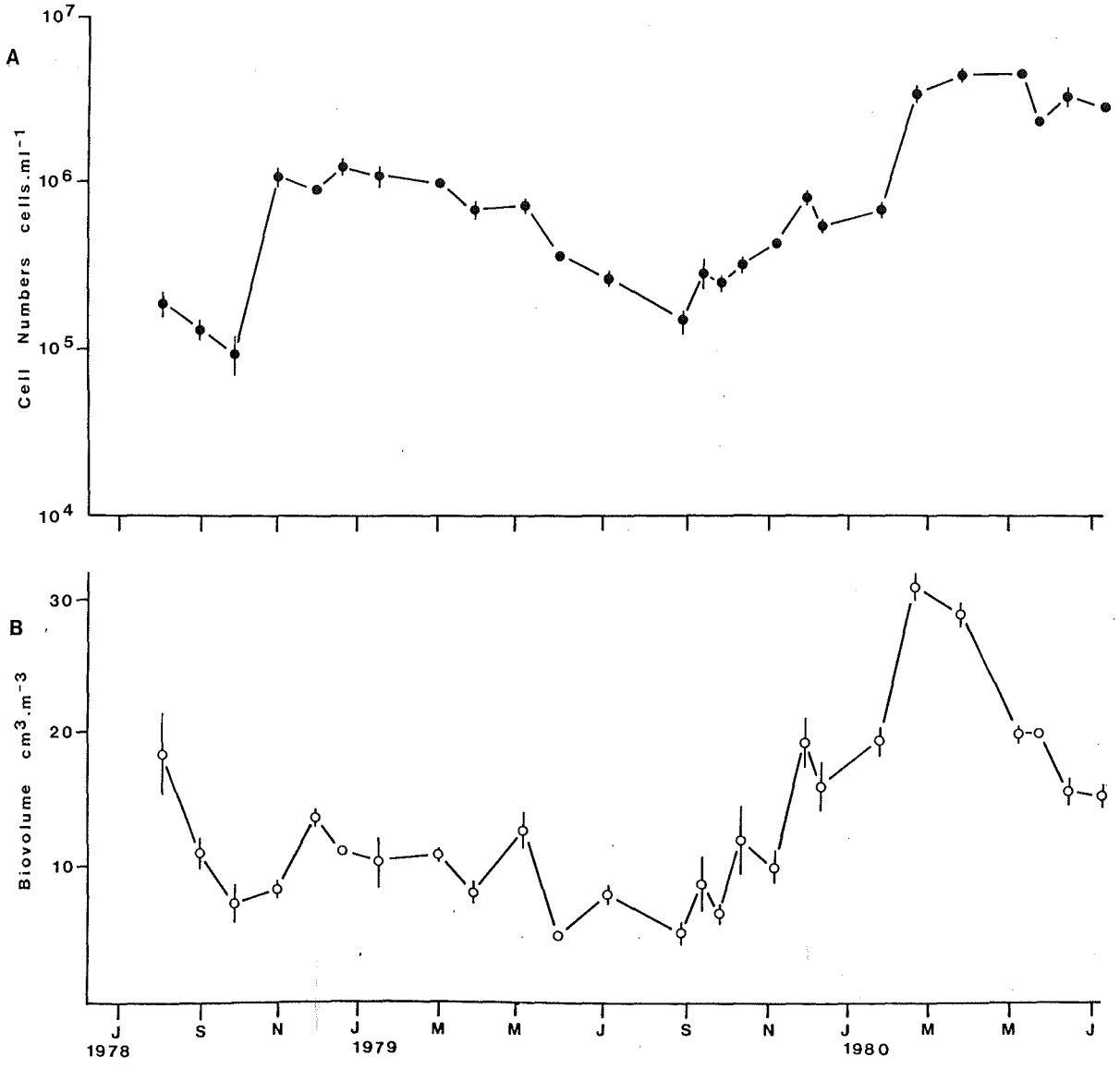


Figure 6/4: Total Standing Crop

A. Cell Numbers (±S.E.)

B. Biovolume (±S.E.)

in August 1979 at 5.29 $cm^3.m^{-3}$, but the lowest biovolume for any one site was 0.40 $cm^3.m^{-3}$ from site 13 (near the outflow) in December 1979. On this occasion, seawater had flowed into the lake (see section 4.2.1) and consequently few phytoplankton species were recorded (see section 6.2).

The mean total biovolumes for most of the individual species over the two year period (July 1978-1980) are shown in Figures 6/5 to 6/13. These have been calculated as the mean over the whole lake for each collecting trip. Different vertical scales are used in Figures 6/5 to 6/7 than are used in Figures 6/8 to 6/13. Uniformity of scale within the two separate series of graphs permits comparison of the populations. Species which recorded a mean volume greater than 2.0 $cm^3.m^{-3}$ are in Figures 6/5 - 6/7, and those with a smaller biovolume are shown in Figures 6/8 - 6/13. Several of the most rare species which made a very small contribution to the biovolume in any one collection have not been shown.

6.3.1 Abundant Species

The most abundant species were Dictyosphaerium primarium, D. pulchellum, Oocystis parva, O. lacustris, Planctonema lauterborni and Microcystis minutissima. With the exception of Microcystis minutissima, this group of abundant species is the same as the group of frequent species described on the basis of presence-absence data. By implication the species which dominate within the phytoplankton flora are present for most of the time. Yet a visual appraisal of the biovolume graphs shows that each of these species shows wide variations in standing crop.

Oocystis parva (including O. marssonii; see Chapter 5 for explanation) (Fig. 6/5B) were the organisms with the single greatest mean biovolume at any one time over the two year period. It was in February 1980 that their mean biovolume reached 12.53 $cm^3.m^{-3}$. The maximum at any single site was 14.82 $cm^3.m^{-3}$ and this was recorded at the same time. The population peak attained during this summer period was greatly in excess of the previous year. It is difficult to distinguish a clear annual cycle for these species.

Oocystis lacustris (Fig. 6/5A) shows a pattern similar to that of the other Oocystis species. This species was at generally low levels from 1978 until early 1979, but increased in spring to attain

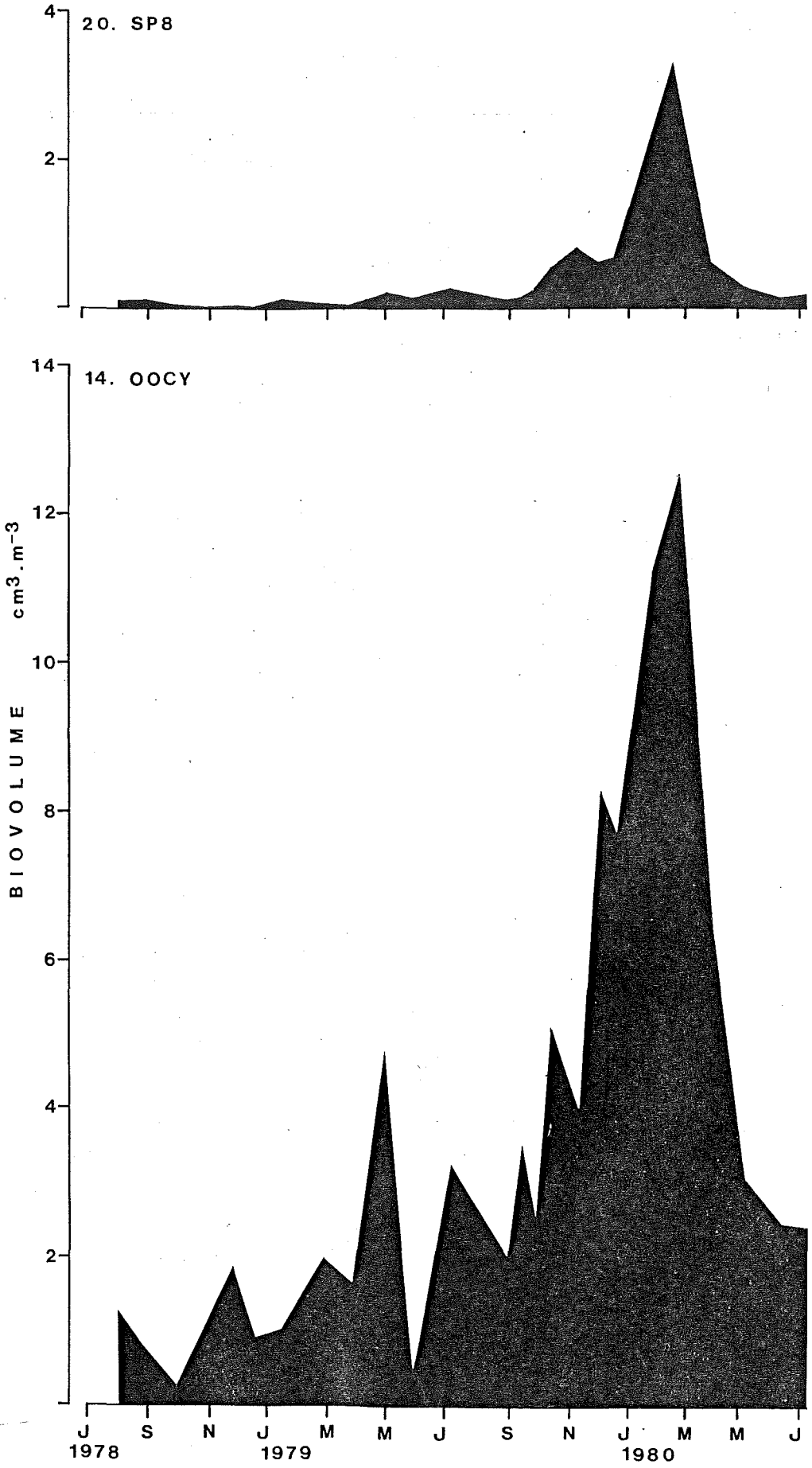


Figure 6/5: Species Biovolume
20. SP8 Oocystis lacustris
14. OOCY Oocystis parva

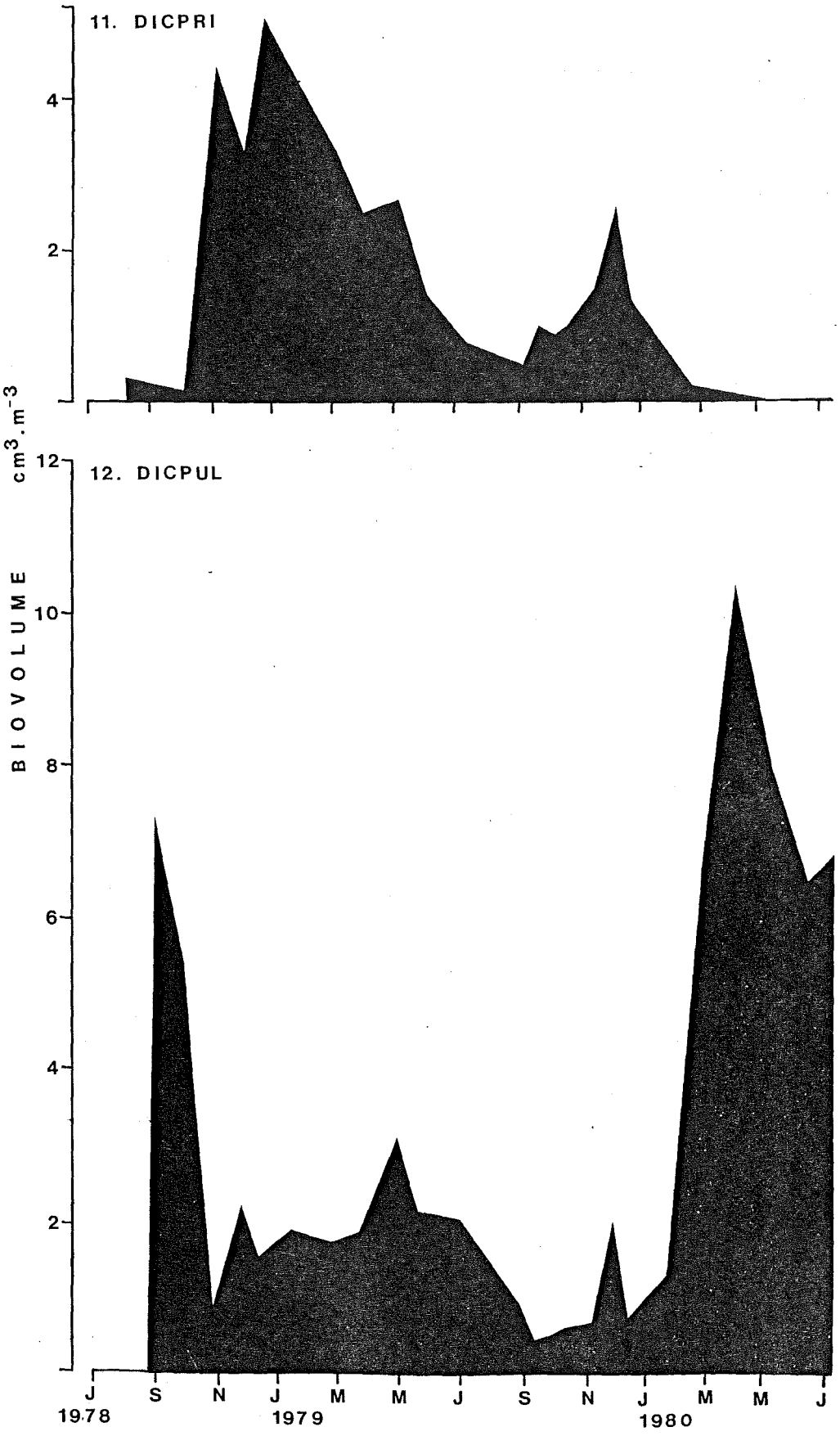


Figure 6/6: Species Biovolume
11. DICPRI Dictyosphaerium primarium
12. DICPUL Dictyosphaerium pulchellum

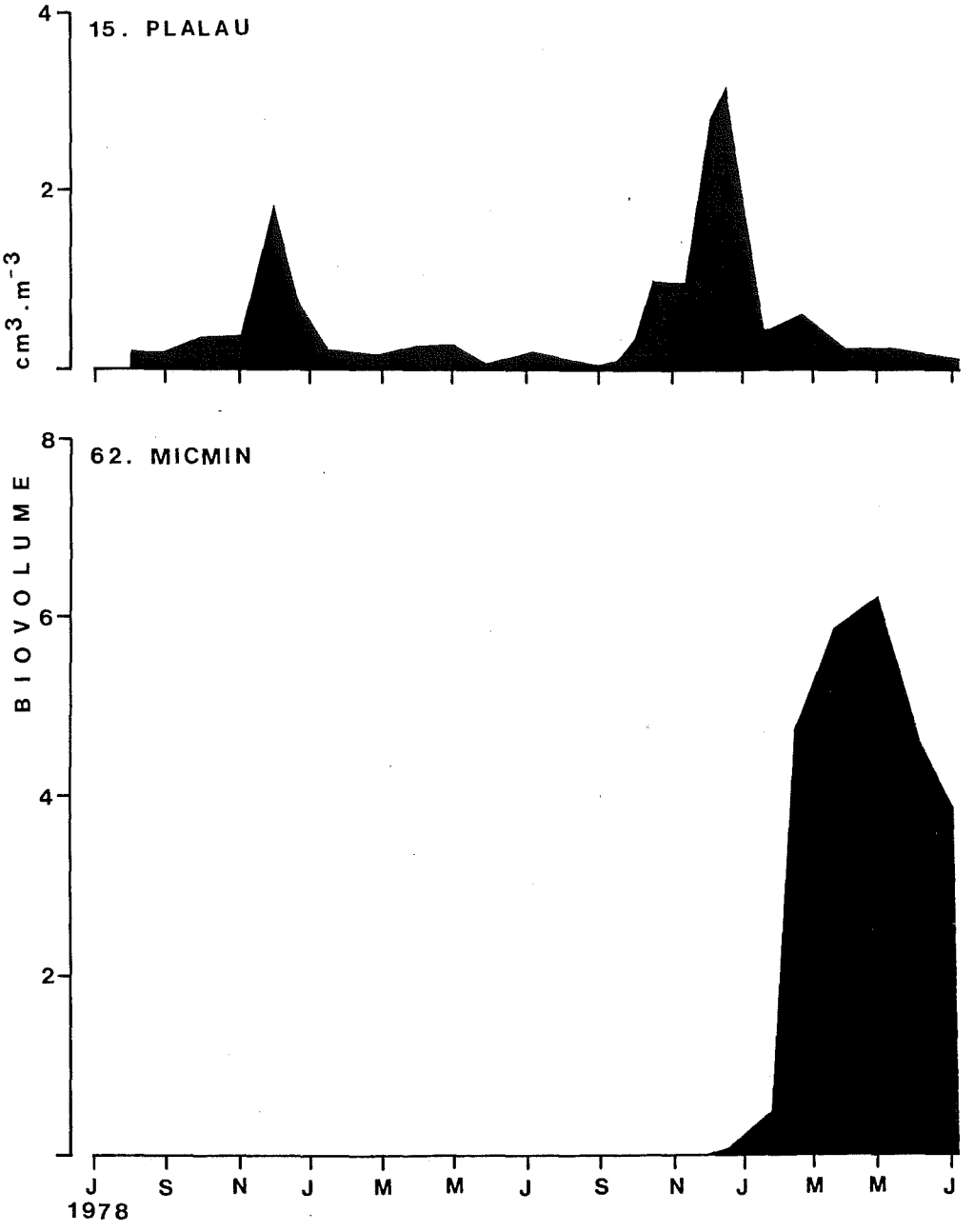


Figure 6/7: Species Biovolume
15. PLALAU Planctonema lauterborni
16. MICMIN Microcystis minutissima

a maximum mean biovolume of 3.22 $cm^3.m^{-3}$ in February 1980. After this peak the levels declined towards the end of the sampling period. The maximum biovolume recorded for this species was 4.13 $cm^3.m^{-3}$ for sites 5 and 10, in February 1980.

Dictyosphaerium primarium (Fig. 6/6A) was the only species present in every sample collected from Lake Ellesmere (see Table 6/2), and was the major dominant organism over the summer of 1978-1979. The standing crop of this species was at its peak in December 1978, at 5.04 $cm^3.m^{-3}$. The maximum for any site at the time was 6.03 $cm^3.m^{-3}$ for site 14, but a higher level of 7.33 $cm^3.m^{-3}$ had been recorded at site 11 in October 1978. During winter 1979 the standing crop of Dictyosphaerium primarium reduced, but it rose again in the spring of 1979. The mean in the summer of 1979-1980 was only 2.56 $cm^3.m^{-3}$. Subsequently there was a decline to the very low level of 0.039 $cm^3.m^{-3}$ in May 1980.

Dictyosphaerium pulchellum (Fig. 6/6B), which has larger cells than D. primarium, shows a quite different population pattern. After a phase of declining biovolume in the early stages of the sampling period, the population stabilised through the first half of 1979. There was a slight peak in May 1979. The population declined further during the spring, but then it rose to very high levels in late summer and remained high into winter 1980. The highest mean population size was 10.34 $cm^3.m^{-3}$ in late March 1980. At Site 2, a level of 14.87 $cm^3.m^{-3}$ was recorded at this time. This was the highest density of any individual species in any single sample and was marginally higher than Oocystis parva. The lowest mean level was in September 1979 at 0.43 $cm^3.m^{-3}$. Over all the 206 samples, this species was absent from only five samples.

Planctonema lauterborni (Fig. 6/7A) was the only abundant species to show a marked seasonal cycle in both years. In the spring and summer of both years the standing crop rose to a peak in late November or December. The mean biovolume in the second year, December 1979, was the greater, at 3.20 $cm^3.m^{-3}$. The maximum for any one site

was the biovolume of 6.53 $cm^3.m^{-3}$ recorded at Site 10 in that collection. The lowest mean level was in August 1979 when the mean biovolume was 0.084 $cm^3.m^{-3}$.

Microcystis minutissima (Fig. 6/7B) was the only non-chlorophyte abundant species. After being absent for most of 1978 and 1979, it was briefly recorded in May, July and September 1979. From late November 1979, the standing crop rose rapidly to its peak mean biovolume of 6.19 $cm^3.m^{-3}$ in May 1980. At site 14, the maximum level of 7.83 $cm^3.m^{-3}$ was recorded at this same time.

It is difficult to distinguish any pattern amongst these abundant species. Dictyosphaerium primarium was dominant during the summer of 1978-1979, and Planctonema lauterborni experienced a brief dominance early in the summer. During autumn 1979 Dictyosphaerium primarium declined, but in the winter it was still sub-dominant along with Dictyosphaerium pulchellum, while Oocystis species were dominant.

In the spring of 1979 there was a massive increase in the standing crop. Oocystis species were largely dominant through the early part of summer until late February 1980. At this time there was a succession of sub-dominants including Dictyosphaerium primarium at first and then Planctonema lauterborni. Oocystis species declined rapidly after February 1980, and Dictyosphaerium pulchellum was then the dominant species. By early May this population was declining, at which time Microcystis minutissima was a significant subdominant organism. The standing crop at the end of the study was still large, dominated by Dictyosphaerium pulchellum.

6.3.2 Minor Species

Any species which did not reach a mean biovolume of 2.0 $cm^3.m^{-3}$ at any time was regarded quite arbitrarily as a minor species. This method of sorting species may be queried because some species such as Lobocystis sp. and Unknown sp. S56 were for brief periods abundant throughout the lake and were obviously sub-dominants, although not necessarily present at all times. Figures 6/8 to 6/13 show the mean biovolumes for the more important minor species. It is not necessary to discuss each species in detail, but similarities and differences

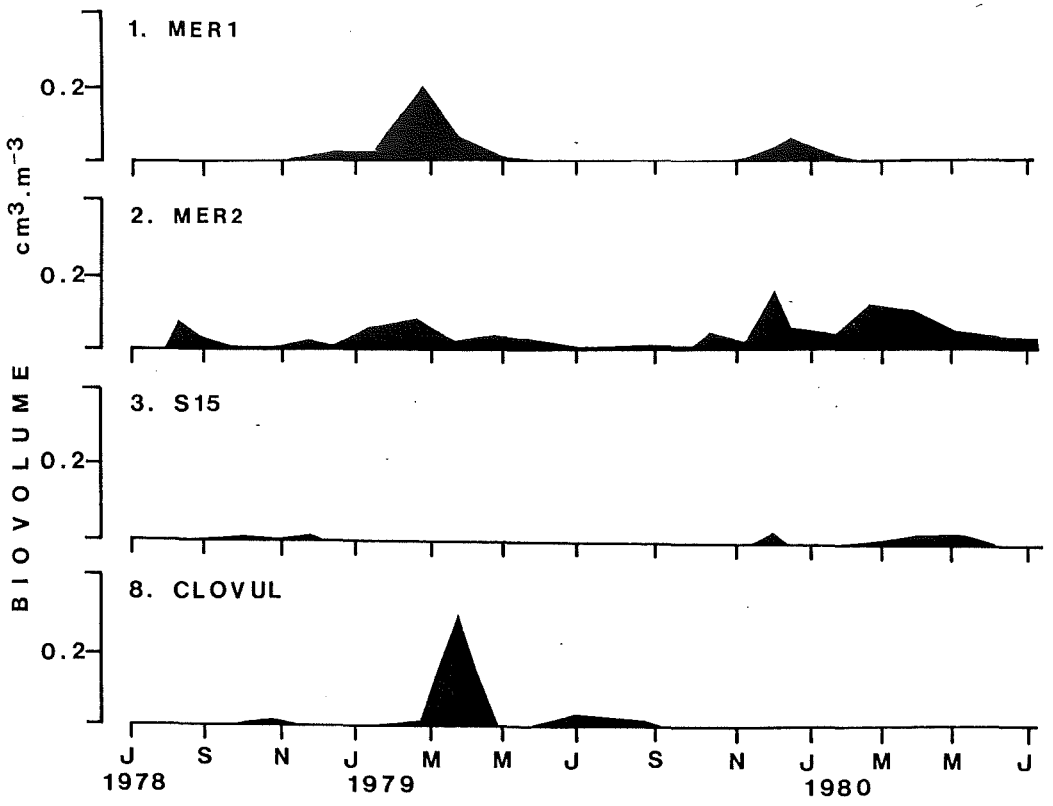


Figure 6/8: Species Biovolume

1. MER1 Merismopedia tenuissima
2. MER2 Merismopedia punctata
3. S15 Unknown sp. S15
8. CLOVUL Chlorella vulgaris

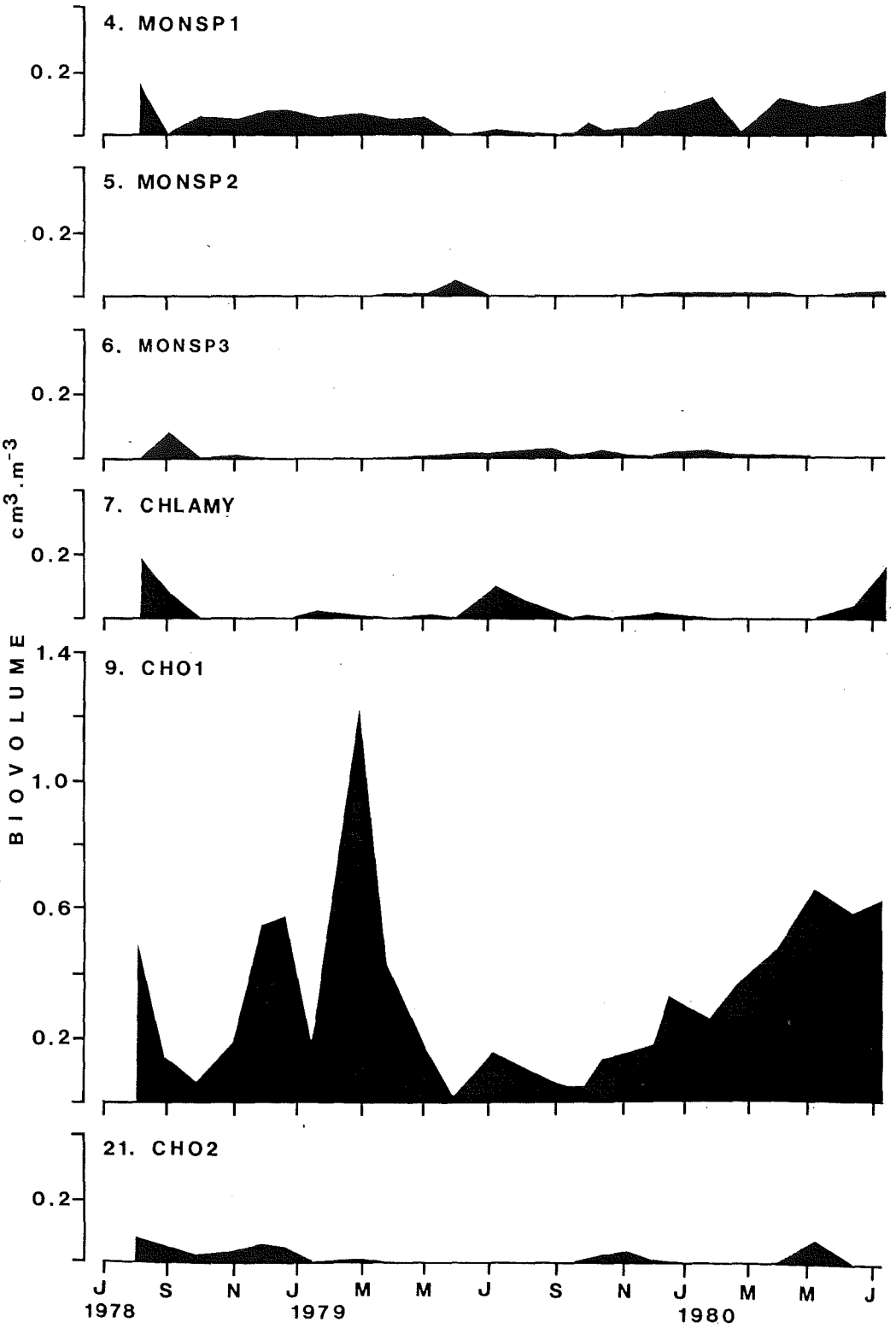


Figure 6/9: Species Biovolume

4.	MONSP1	Monoraphidium contortum
5.	MONSP2	Monoraphidium minutum
6.	MONSP3	Monoraphidium griffithii
7.	CHLAMY	Chlamydomonas sp.
9.	CHO1	Chodatella quadriseta
21.	CHO2	Chodatella subsalsa

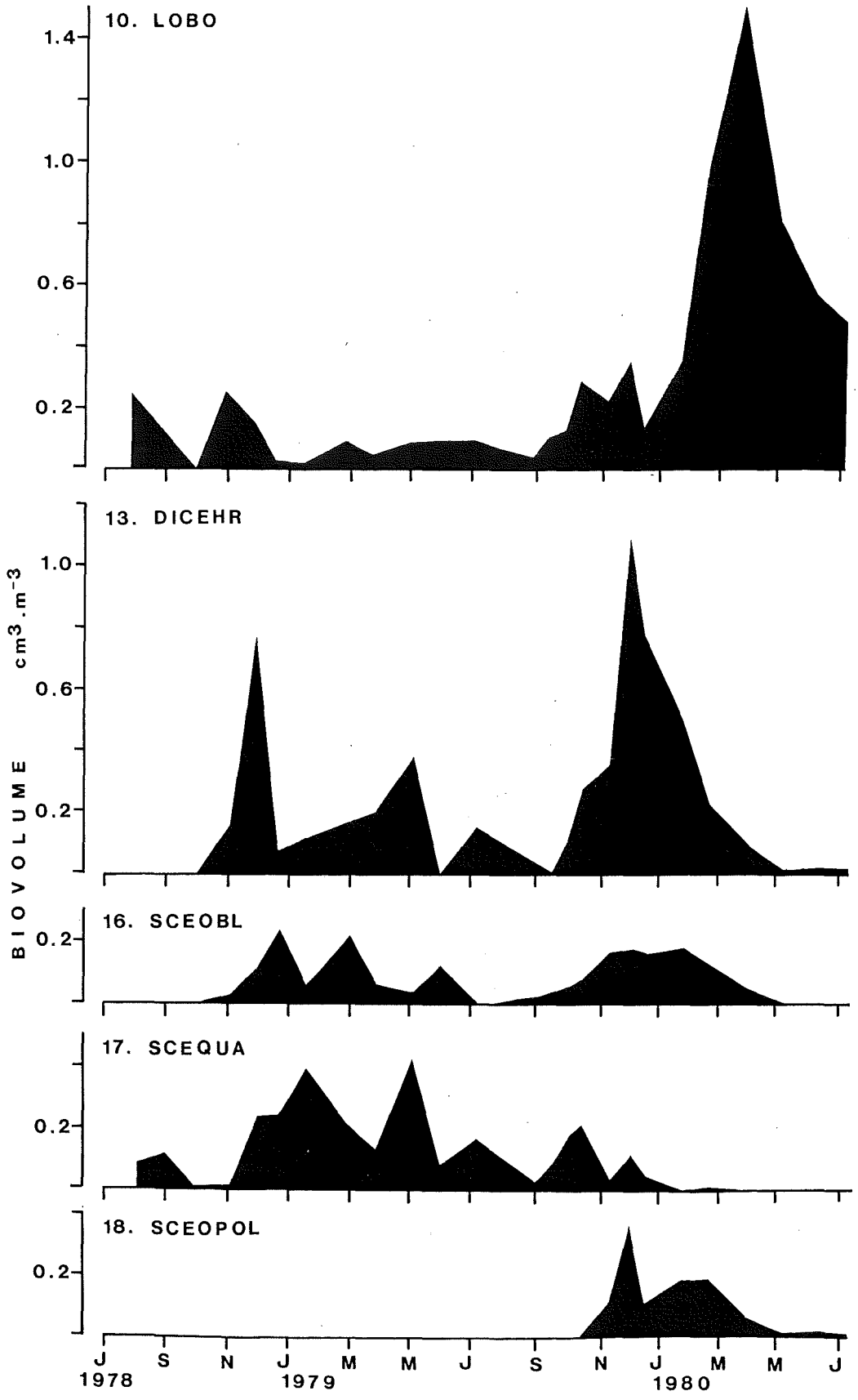


Figure 6/10: Species Biovolume

10.	LOBO	Lobocystis sp.
13.	DICEHR	Dictyosphaerium ehrenbergianum
16.	SCEOBL	Scenedesmus obliquus
17.	SCEQUA	Scenedesmus quadricauda
18.	SCEOPOL	Scenedesmus opoliensis

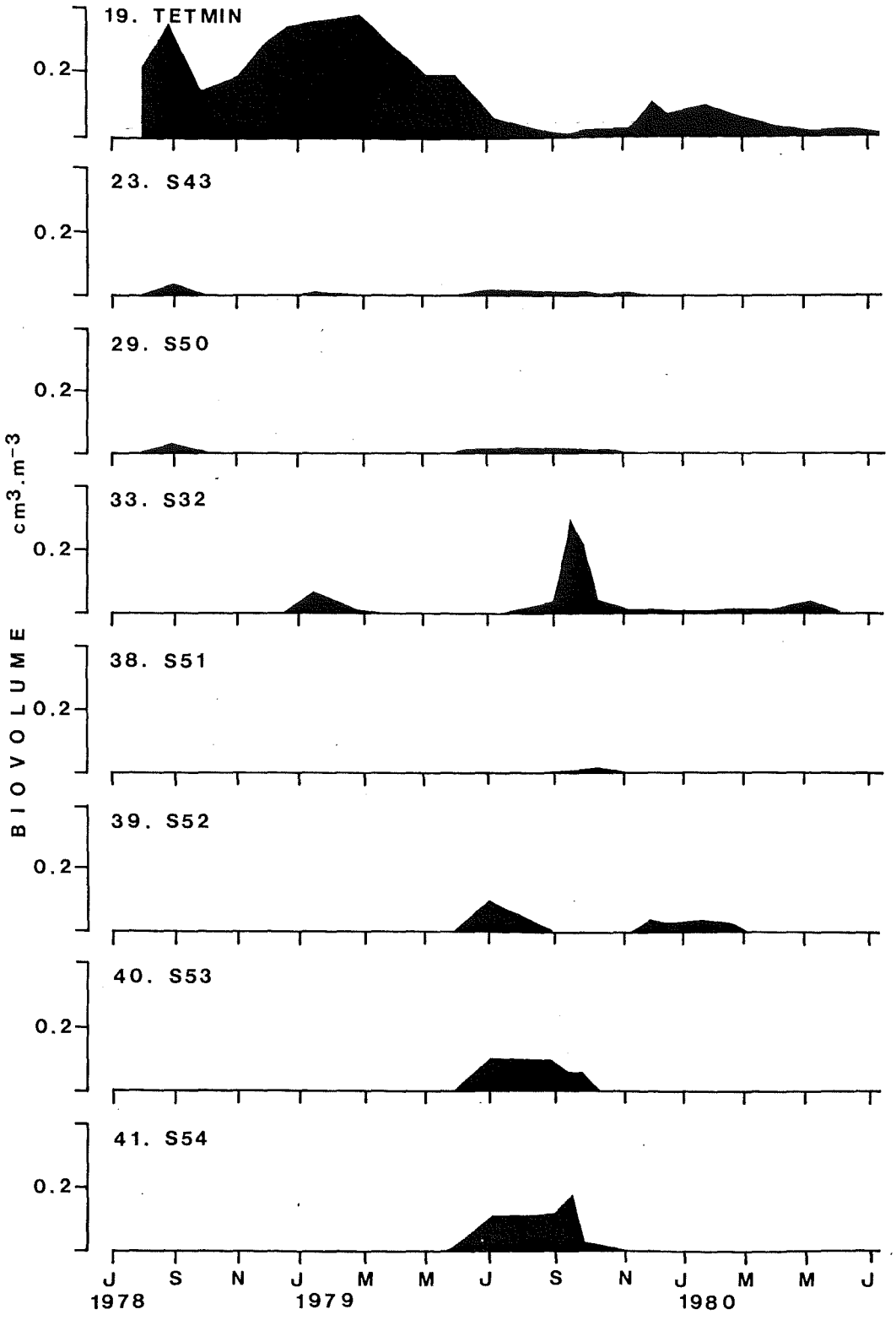


Figure 6/11: Species Biovolume

19 TETMIN	Tetraedron minimum:
23 S43	Unknown sp. S43
29 S50	Unknown sp. S50
33 S32	Unknown sp. S32
38 S51	Unknown sp. S51
39 S52	Unknown sp. S52
40 S53	Unknown sp. S53
41 S54	Unknown sp. S54

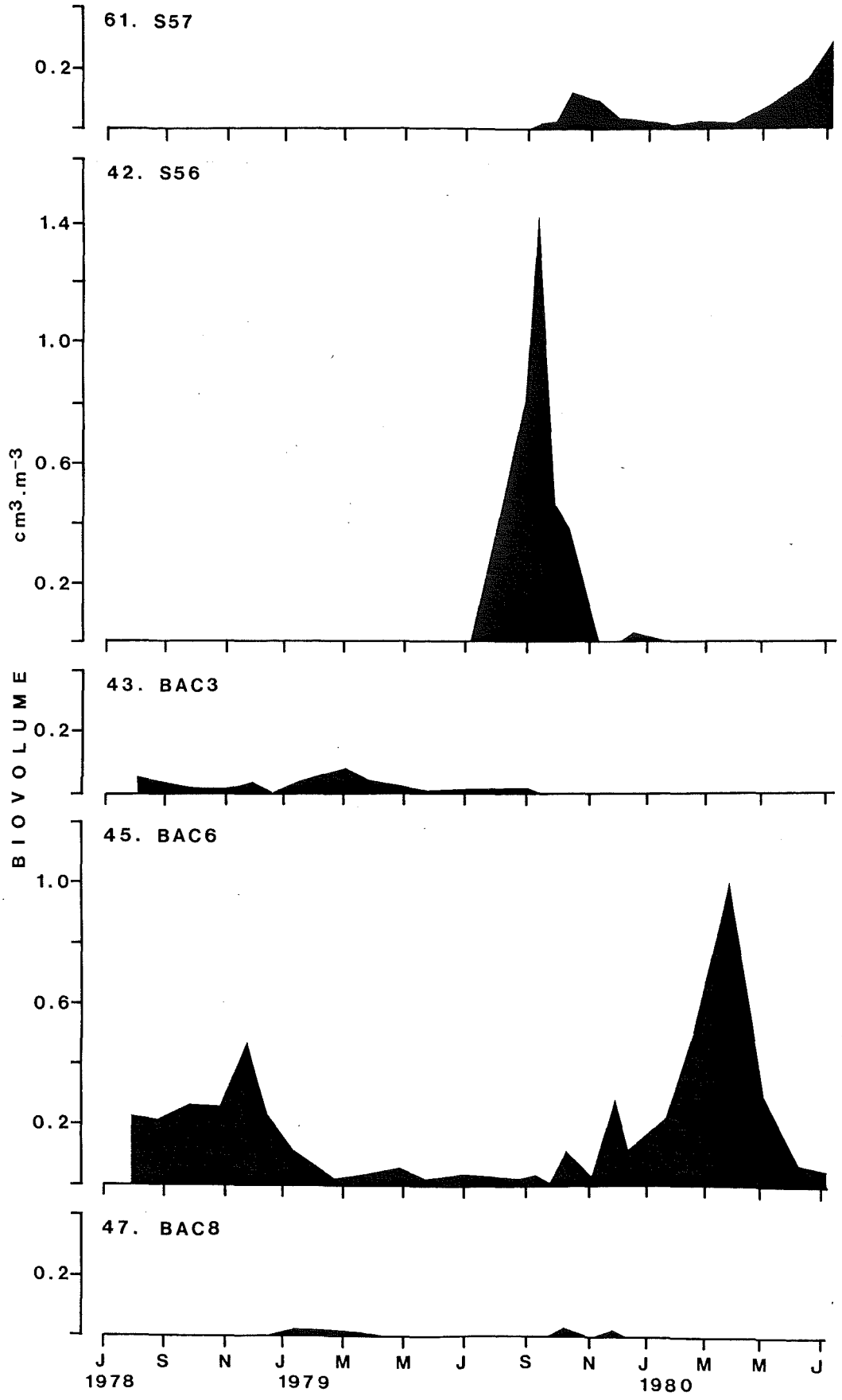


Figure 6/12: Species Biovolume
61. S57 Unknown sp. S57
42. S56 Unknown sp. S56
43. BAC3 Pennate diatoms 3
45. BAC6 Pennate diatoms 6
47. BAC8 Pennate diatoms 8

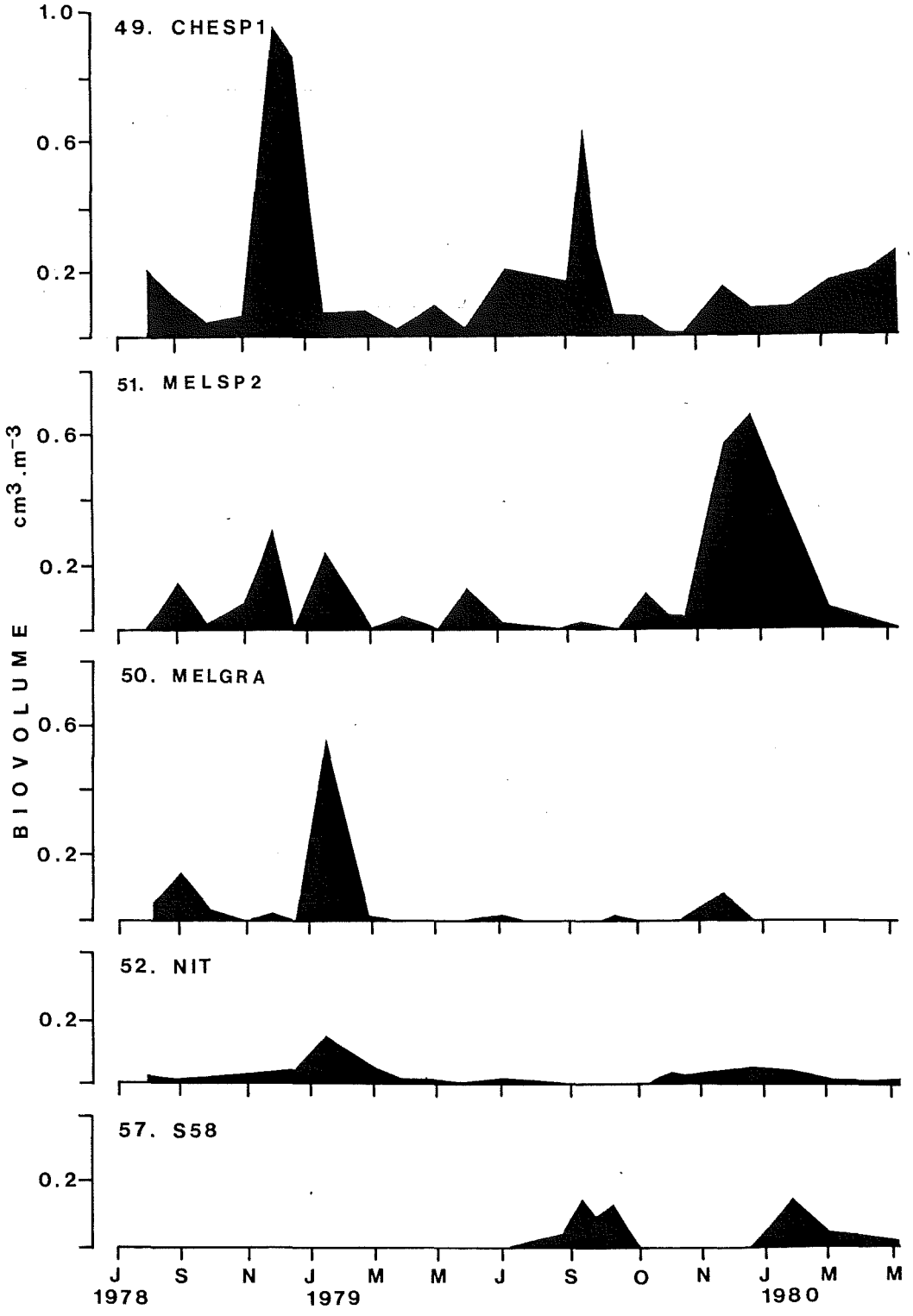


Figure 6/13: Species Biovolume
49 CHESP1 Chaetoceros spl
51 MELSP2 Melosira sp2
50 MELGRA Melosira granulata
52 NIT Nitzschia sp.
57 S58 Unknown sp.S58

between groups of organisms need to be drawn out. The complex and dynamic nature of the phytoplankton community can only be fully appreciated when the contribution of these minor species is borne in mind.

The first group of minor species were the frequent species (see section 6.2) present for all or most of the period surveyed. This included many of the green algae group such as Monoraphidium contortum (Fig. 6/9), Lobocystis sp. (Fig. 6/10), Chodatella quadriseta (Fig. 6/9), Dictyosphaerium ehrenbergianum (Fig. 6/10), Scenedesmus spp. (Fig. 6/10), and Tetraedron minimum (Fig. 6/11). Also included in this group were several diatom size classes and species, such as BAC6 (Fig 6/12), Chaetoceros sp. (Fig. 6/13) and Melosira sp2 (Fig. 6/13). The individual species within this group often showed seasonal fluctuations at different times of the year. For example, Dictyosphaerium ehrenbergianum was most abundant during the spring and summer, whereas Chodatella quadriseta was more abundant during the autumn and winter period. Other species, for example Scenedesmus quadricauda and Tetraedron minimum, were more abundant in one year but not the other. Taken as a whole however, the dispersed nature of this group meant that they contributed very little to the total biovolume of the lake.

The second group of minor species were chiefly infrequent species (see section 6.2) that appeared in the lake for short periods at a time, but staged at least one reappearance. This group included the Cyanophyta: Merismopedia tenuissima (Fig. 6/8) and Unknown sp. S15 (Fig. 6/8); the Chlorophyta: Chlorella vulgaris (Fig. 6/8), Monoraphidium minutum (Fig. 6/9), M. griffithii (Fig. 6/9), Chlamydomonas sp. (Fig. 6/9), Chodatella sp2. (Fig. 6/9), and Unknown sp S43 (Fig. 6/11). Diatoms in this group included: BAC3 (Fig. 6/12), BAC8 (Fig. 6/12), Melosira granulata (Fig. 6/13) and Nitzschia sp. (Fig 6/13); and the Cryptophyta: Unknown sp. S58 (Fig. 6/13). The species of this group rarely reached high levels. Most of the time they were either absent or at low levels. Only two species contributed more than 0.2 $cm^3.m^{-3}$ to the mean biovolume for any period. These were Chlorella vulgaris at 0.29 $cm^3.m^{-3}$ in March 1979, and Melosira granulata at 0.56 $cm^3.m^{-3}$ in January 1979.

The third group of minor species were present in the lake at only one period during the collection of data. This group was almost entirely made up of members of the Chrysophyceae which appeared in the lake between May and November 1979. Some of the species, for example Unknown sp. S56 (Fig. 6/12), briefly attained quite high standing crops before declining and disappearing again. Unknown sp.S57 (Fig 6/12) continued after this time and its population size had begun to increase again at the end of the period.

The fourth and final group of minor species were even more elusive. This group is similar to the rare group discussed previously (see section 6.2) and have not been presented graphically. Most of these entities were unnamed and could not be adequately described because of the paucity of samples. Although rare, some of this group contributed significantly to the total biovolume of individual samples. In particular the larger diatoms and dinoflagellate deserve mention. For example one specimen of Gymnodinium sp. had a biovolume of 0.014 cm^3.

The four groups of minor species played a complex role within the phytoplankton community. Some species appeared at different times of the same year, or appeared in different times in different years. Changes in biovolume of these species, along with changes in the abundant, dominant species (section 6.3.1) make the patterns difficult to interpret without the aid of a multivariate data reduction method. This method is applied to this same data in the next section.

6.4 MULTIVARIATE ANALYSIS OF COMMUNITY STRUCTURE

Multivariate statistical analysis has the ability to reduce complexity within a data set by finding underlying patterns within the variables. Terrestrial plant ecologists have developed several multivariate techniques to analyse complex ecological data sets, particularly with reference to environmental gradients. Whittaker (ed., 1978) has a useful discussion of several different approaches to ordination (i.e. arrangement of samples in relation to environmental gradients). Algal ecologists have been slower to adopt similar approaches as a way of summarizing community analysis (Allen and Skagen, 1973).

The most commonly used multivariate technique for phytoplankton data has been principal component analysis, an indirect ordination method (Symons, 1970; Allen and Koonce, 1973; Holland and Clafflin, 1975; Hillebrand, 1978; Harris and Piccinin, 1980). However, this method of ordination has been strongly criticised as inappropriate for ecological data (Beals, 1973), because it does not take account of the normal distribution of success of species relative to the environment, and because it does not take due notice of species absence. Other techniques have been developed and used by aquatic ecologists including: position vector ordination (Levandowsky, 1972), polar ordination (Allen and Skagen, 1973; Baybutt and Makarewicz, 1981), and reciprocal averaging (Happey-Wood, 1980; Baybutt and Makarewicz, 1981).

Reciprocal averaging (RA) is a weighted average ordination effected by successive approximations which was developed by Hill (1973). It is used, when there are a number of observations, to reveal correspondences between two kinds of information, such as species and samples (Gauch et al., 1977). It is an eigenvector technique and therefore it is related to principal component analysis (PCA). Comparison between the two techniques, RA and PCA, has shown that the former gives similar but more meaningful ecological results (Hill, 1973; Gauch et al., 1977).

Reciprocal averaging has two major drawbacks (Hill and Gauch, 1980). The worst is the 'arch effect', which is a mathematical artifact and arises because the second axis is constrained so that while it is uncorrelated with the first axis, it is not independent of it. This makes interpretation of separate axes difficult. The other main fault with RA is the non-equivalence of ecological distances at the ends of the axes.

An improved technique to overcome the two drawbacks in reciprocal averaging is detrended correspondence analysis (DCA) (Hill and Gauch, 1980). Gauch et al. (1981) have shown the superiority of DCA over both RA and other ordination methods, and suggested its applicability for ecological data. Unfortunately DCA was not available for use at the time of this study, so a version of RA has been used (H/RECIPAVER, see section 2.4).

Reciprocal averaging was carried out on the biovolume data set of 206 samples for 61 species. The data was standardized and the species

occurring in fewer than 10% of the samples were down-weighted. This down-weighting, which is designed to reduce the influence of rare species on the ordination, involves altering values by the square of their frequency. No down-weighting of species-poor stands was undertaken.

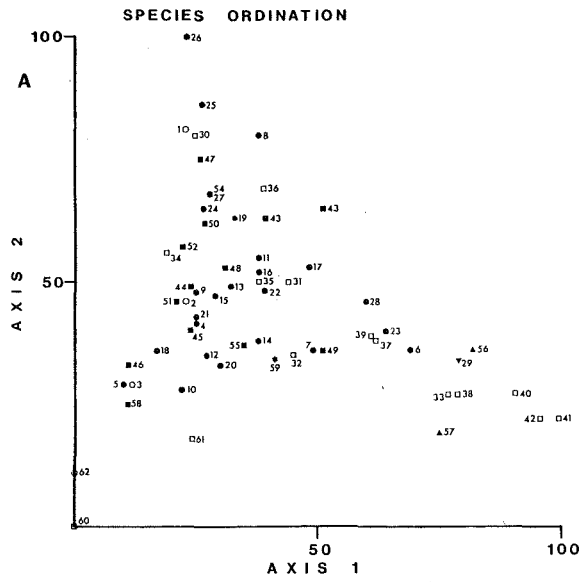
The variability produced by successive axes extracted from the data was expressed as eigenvalues. The eigenvalues for the first twenty axes are given in Table 6/14, as are the proportion of variability and the cumulative proportion for the axes. Unfortunately the RECIPAVER program does not calculate the variation of the data matrix which is still unexplained. The proportion variability and cumulative proportion of the variability therefore vary according to the number of axes extracted from the data. Although the eigenvalues remain the same, the proportion of the variability can only be estimated from the sum total of all of the eigenvalues. In the present analysis, based on twenty axes, 38% of the variability is accounted for by the first three axes. If only five axes were extracted the first three axes would account for over 71% of the variability. If ten axes had been extracted, the first three axes would seem to account for 51% of the variability, so the residual variability within the analysis must not be neglected. The trend in the eigenvalues as seen in Table 6/14 suggests that considerable variability may still remain unaccounted after the extraction of the first twenty axes.

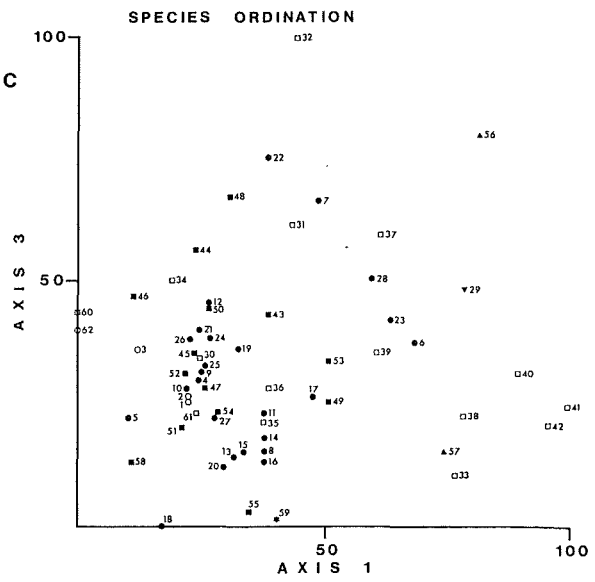
The species and sample ordinations are presented in Figures 6/15 and 6/16 for each pair of the first three axes. The two series of axis pairs have a similar scatter of the data and a consequent similarity of scatter in hyperspace, due to the technique of extracting the correspondence between both kinds of information. Thus the axes of both series are directly comparable.

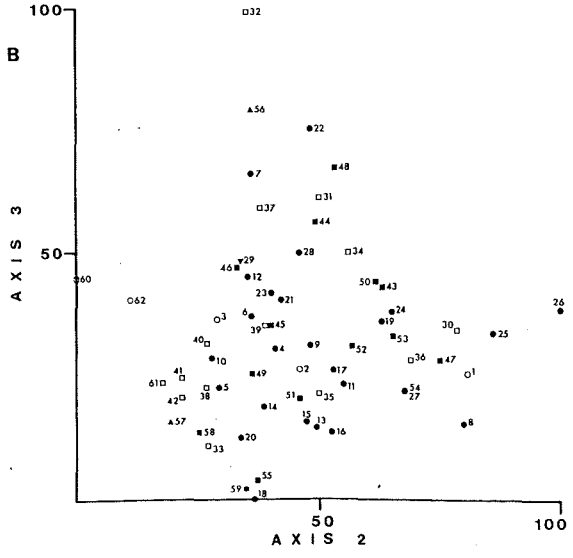
The first two axes (Figs. 6/15A and 6/16A) show a three pointed scatter of the data. Most of the samples and species are at the lower end of the first axis. There is no evidence of the kind of noticeable 'arch' effect which would be produced by the mathematical artifact of the method if any underlying factor had dominated this first axis. The second and third axes (Figs. 6/15B, and 6/16B) show a wider scatter of data, with isolated samples and

Table 6/14: Eigenvalues of the first twenty axes.

Axis	Eigenvalue	Proportion of variability	Cumulative Proportion
1	.304	14.84	14.84
2	.270	13.18	28.02
3	.210	10.25	38.27
4	.158	7.71	45.98
5	.141	6.88	52.86
6	.117	5.71	58.57
7	.095	4.63	63.20
8	.087	4.24	67.44
9	.077	3.75	71.19
10	.073	3.56	74.75
11	.069	3.36	78.11
12	.064	3.12	81.23
13	.060	2.92	84.15
14	.054	2.63	86.78
15	.052	2.53	89.31
16	.051	2.49	92.21
17	.043	2.09	94.30
18	.043	2.09	96.39
19	.040	1.95	98.34
20	.040	1.95	100.29
	2.048		





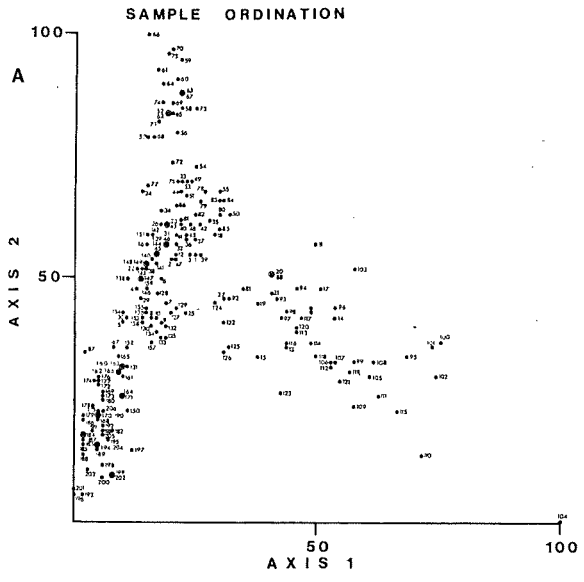


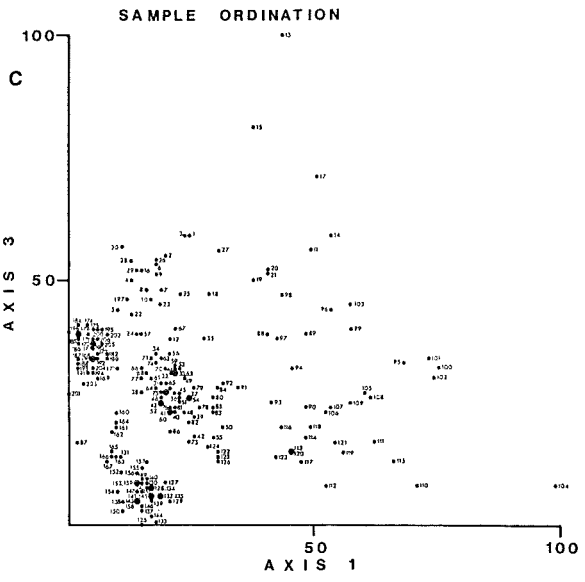
Key:

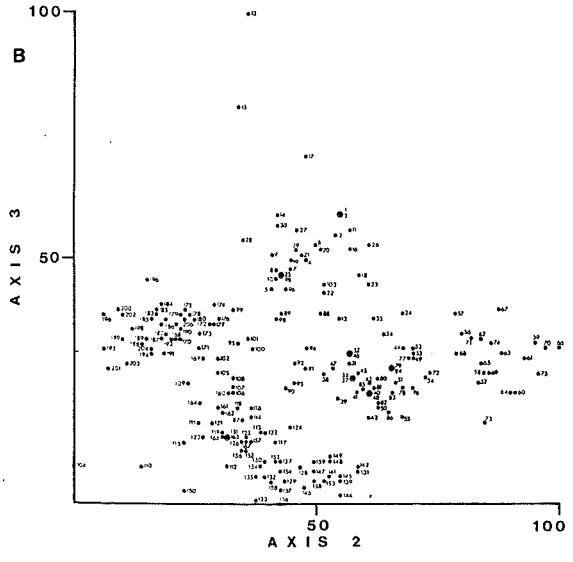
Spp. No.	Taxonomic	Code name[1]	Spp. No.	Taxonomic	Code name	Spp. No.	Taxonomic	Code name
1	○ Cyanophyta	MER1	18		SCEOPOL	41		S54
2		MER2	19		TETMIN	42		S56
3		S15	22		S11	60		S60
62		MICMIN	23		S43	61		S61
4	● Chlorophyta	MONSP1	24		S44	43	■ Diatomophyceae	BAC3
5		MONSP2	26		S47	44		BAC4
6		MONSP3	27		CRU	45		BAC6
7		CHLAMY	28		ACT	46		BAC7
8		CLOVUL	29	▼ Euglenophyceae	S50	47		BAC8
9		CHO1	30	□ Chrysophyceae	S21	58		BAC12
21		CHO2	31		S22	48		BAC10
10		LOBO	32		S24	49		CHESP1
11		DICPR1	33		S32	54		CHESP2
12		DICPUL	34		S40	50		MELGRA
13		DICEHR	35		S42	51		MELSP1
14		OOCY	36		S46	52		VLT
20		SP8	37		S48	53		AMP
15		PLALAU	38		S51	55		COS
16		SCEOBL	39		S52	56	▲ Cryptophyceae	S26
17		SCEQUA	40		S53	57		S58
						59	◆ Dinophyceae	DINO

[1] Code name as given in Table 6/1.

Figure 6/15: Species Ordination
A. Axes 1 and 2
B. Axes 2 and 3
C. Axes 1 and 3
An enlarged copy of this figure is given as Supplementary Figure 4.







Key:

Ord No	Coll No	Site No	Ord No	Coll No	Site No	Ord No	Coll No	Site No	Ord No	Coll No	Site No	Ord No	Coll No	Site No
1	2	1	42		6	83		8	124	17	1	165		8
2		2	43		8	84		10	125		2	166		10
3		5	44		10	85		11	126		11	167		13
4		6	45		11	86		12	127	18	1	168	23	1
5		8	46		12	87	12	4	128		2	169		2
6		10	47		13	88	13	1	129		4	170		4
7		11	48		14	89		2	130		5	171		5
8		12	49	7	2	90		4	131		6	172		6
9		13	50		5	91		5	132		8	173		8
10		14	51		14	92		6	133		10	174		10
11	3	1	52	8	6	93		8	134		11	175		11
12		2	53		8	94		10	135		12	176		12
13		4	54		10	95		11	136		13	177		14
14		5	55		11	96		12	137		14	178	24	1
15		6	56		12	97		13	138	19	1	179		2
16		8	57		13	98		14	139		2	180		4
17		10	58		14	99	14	1	140		11	181		5
18		11	59	9	1	100		2	141	20	1	182		6
19		12	60		2	101		4	142		2	183		8
20		13	61		4	102		5	143		5	184		10
21		14	62		5	103		6	144		5	185		12
22	4	1	63		6	104		8	145		6	186		13
23		2	64		8	105		10	146		8	187		14
24		4	65		10	106		11	147		10	188	25	1
25		6	66		11	107		12	148		11	189		2
26		8	67		12	108		13	149		12	190		3
27		10	68		13	109		14	150		13	191		5
28		11	69		14	110	15	1	151		14	192		6
29		12	70	10	1	111		2	152	21	4	193		8
30		14	71		2	112		11	153		6	194		10
31	5	1	72		5	113	16	1	154		8	195		11
32		2	73		6	114		2	155		10	196		13
33		4	74		10	115		4	156		11	197	26	1
34		5	75		12	116		5	157		12	198		2
35		6	76		13	117		6	158		13	199		4
36		10	77		14	118		8	159		14	200		6
37		11	78	11	1	119		10	160	22	1	201		8
38		14	79		2	120		11	161		2	202		10
39	6	2	80		4	121		12	162		4	203		11
40		4	81		5	122		13	163		5	204		12
41		5	82		6	123		14	164		6	205		13
												206		14

Figure 6/16: Sample Ordination
A. Axes 1 and 2
B. Axes 2 and 3
C. Axes 1 and 3
An enlarged copy of this figure is given as Supplementary Figure 5.

species at the extremes, whereas the first and third axis ordination plots (Figs. 6/15C and 6/16C) show extreme groups at the low end of both axes.

6.4.1 Species Ordination

The species ordination (Figs. 6/15 A,B,C) shows up differences between the taxonomic groups of organisms. The blue-green algae appear in a narrow band at the low end of Axis 1; in a broad scatter on Axis 2; and in a narrow band on Axis 3. In Figure 6/15C, the two Merismopedia species appear in close proximity. The green algae have a larger number of species, but are generally in a central region on all three axes. They are positioned between 10 and 70 on Axis 1, and above 28 on Axis 2.

The Chrysophyceae are a group which occur in a pattern very different from the other groups in the ordination. On Axis 1 they span the full axis range from 0 to 100, although they tend to cluster in the upper region of the axis. This group of species (Unknown spp. S32, S51, S53, S54, S56) are in close proximity on Axes 2 and 3 (Figs. 6/15B and C). This is the same group which occurred in a time-related manner from May to October 1979 (see section 6.3.2). The sole representative of the Euglenophyceae to be counted in samples, Unknown sp. S50, was also present at about the same time, and is positioned close to the Chrysophyceae on each of the three axes. Other Chrysophyceae are found over a wide band on each of the axes. Unknown sp. S24 is positioned at the extreme of Axis 3, but it is in a central position for the other two axes. Table 6/2 shows that this species occurred only rarely but where it did appear it was in the company of two other rare organisms, Unknown spp. S26 and S11. The Diatomophyceae have a similar but narrower range than that of the Chlorophyceae on each of the axes. On Axis 1, they range from 10 to 51, and on Axes 2 and 3 from 25 to 75 and 4 to 76 respectively.

The group Cryptophyceae all occur close to each other on Axis 1, but they are widely separated on Axes 2 and 3. This difference is consequent on the occurrence pattern of each species. Unknown sp. S58 occurred at much the same time as did the group of Chrysophyceae mentioned above, and it is positioned close to this group on all three

axes, whereas Unknown sp. S26 was very rare, occurring in only 1% of the samples. The sole dinoflagellate was positioned centrally on Axes 1 and 2, but at a low extreme position for Axis 3. It is closely associated with the diatom Coscinodiscus sp. on all three axes.

The analysis of taxonomic groups in relation to the species ordinations have shown some groupings based on the time of occurrence of species. The upper extremes of Axis 1 and Axis 3, in particular, showed groupings of species that occurred at specific times within the sampling period. The species present in most samples, often belonging to the Chlorophyceae and Diatomophyceae, were in a central region on all three axes.

The dominant species, as defined by biovolume (see section 6.3.1), are grouped towards the centre of the scatter on all three axes. The exception is Microcystis minutissima which is more distant on all three axes and is closely associated with Unknown sp. S60, which occurred at a similar time. Because of the standardization procedure used in the analysis, the dominant species were not separated from other species. The very abundant dominant organisms were deliberately prevented from dominating the ordination.

6.4.2 Sample Ordination

On each pair of axes of the sample ordination (Figs. 6/16 A,B,C) the samples are spread out in a similar pattern to the data presented for the species ordination (section 6.4.1). It is not possible, however, to pinpoint individual samples in relation to individual species because of the down-weighting that has been applied to the samples.

Further interpretation of the results is possible when samples collected on the same collecting trip are considered as a single unit, since on any collecting trip similar seasonal and chemical conditions prevail (section 4.2). Figures 6/17 and 6/18 represent Axis pairs 1 and 2, and 1 and 3, as given in Figure 6/16 A and C, but only the ordination position of samples from the same collecting trips are shown.

Comparison of Figures 6/17 and 6/18 indicates that there is a time-related sequence expressed in the sample ordination. Figure

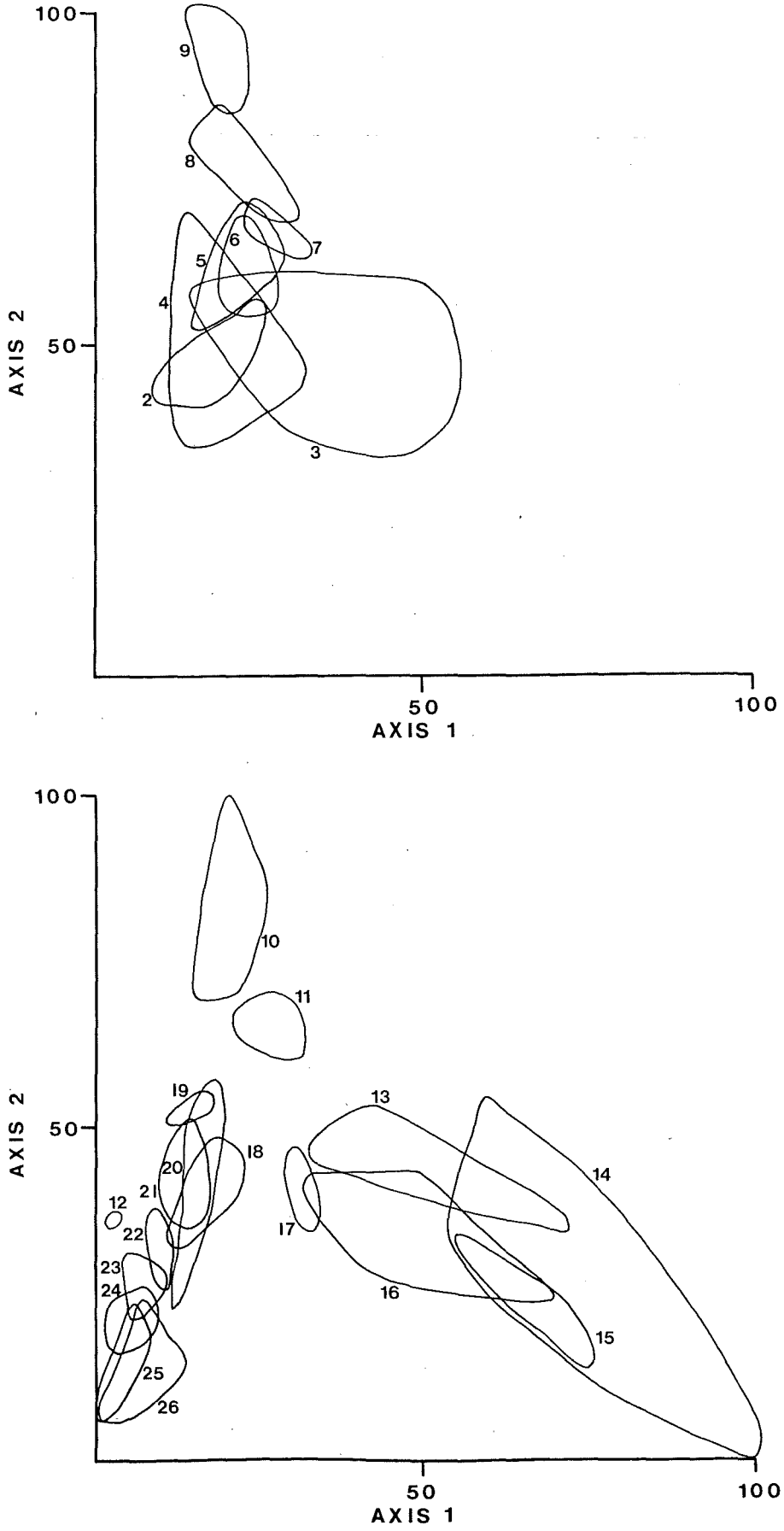


Figure 6/17: Sample Ordination by Collection Number. Axes 1 and 2.

Top: 2-9
Bottom: 10-26
N.B. no phytoplankton analysis of Coll'n 1.

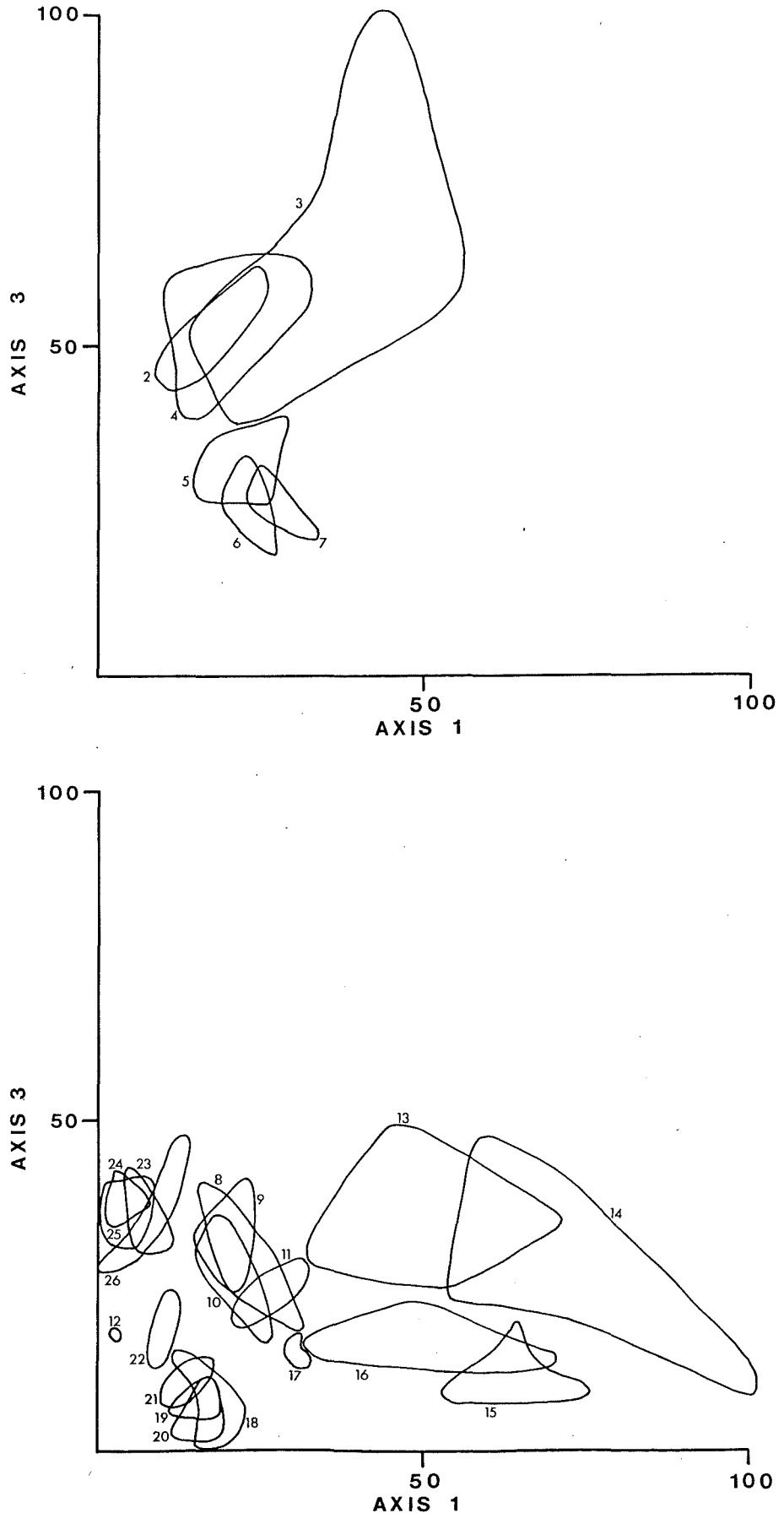


Figure 6/18: Sample Ordination by Collection Number. Axes 1 and 3.

Top: 2-7
Bottom: 8-26
N.B. no phytoplankton analysis of Colln 1.

6/17A shows collecting trips 2 to 9 on the first two axes. A general sequence, particularly along Axis 2, is noticeable from the mid-axis region to the end of the axis. Figure 6/17B shows that samples from collecting trips 10 and 11 form a sequence which tends to move toward the mid-axis region. Collection 12, represented by only one sample, is well removed from a progressive sequence. Samples from collections 13 to 17 form a separate part of the ordination plot, which in itself follows a progression from one to another, while collections 18 to 26 form another sequence which move toward the bottom of both axes.

In Figures 6/18A and B another sequence shows up on Axes 1 and 3. In this case, however, there is more overlap between the ordination position of individual collecting trips. The collections 2 to 4 are more removed than previously, although collections 5 to 11 are essentially clustered in the central region of the figures. Collection 12 is again isolated, as is the sequence associated with collections 13 to 17. There is less noticeable progression between collections 18 to 26, because of the break between collections 22 and 23. The similarity of the sequencing and disjunctions between collection trips in both pairs of axes lends support to the idea that the ordination is time-related.

The scatter of points in the sample ordination indicates the variation between the environment at different sites. Figures 6/18A and B further demonstrate this point. Collections 3 and 14 in particular encircle large regions on the plots. The extreme positions from Collection 3 (samples 13, 14, 15 and 17) are from sites close to inflows at the north-eastern side of the lake. In Collection 14, sample 104 from Site 8 off the Selwyn River has an extreme ordination position. At the time when these collections were made, the phytoplankton flora at these sites were sufficiently distinctive to influence the overall ordination. In the case of sample 104 (Collection 14, Site 8), the phytoplankton was particularly sparse due to freshwater dilution and several of the more common species such as Dictyosphaerium pulchellum were not present (see Table 6/2).

A more detailed analysis of the ecological meaning of the ordination will be given in the next section.

6.4.3 Ecological Interpretation of Ordination Axes

The ordination used in this study has been based on the phytoplankton data. It is possible however to interpret the derived axes from the environmental measurements associated with each sample. One possible method is to use the physico-chemical FACTORS derived earlier (section 4.3) and a second is to use a selection of individual variables.

6.4.3.1 Physico-chemical FACTOR correlation with AXES

It has been shown in a previous section (4.3) that the physico-chemical data, which consisted of 17 variables, can be reduced to five major FACTORS using principal component analysis.

In order to correlate the FACTOR solution with the ordination solution given above the two data sets were amalgamated. The five factors were calculated from the sum of the individual loadings of the 17 variables and these were correlated with axis loadings of the first five ordination axes. Pearson's product moment correlation of the PEARSON CORR subprogram of the SPSS package (SPSS, 1975) was used, but because the normality assumption of this correlation was not fulfilled, no test of significance was applied to the resultant coefficient. The resultant matrix can therefore only be used in a descriptive manner. The correlation of factors with the axes is given in Table 6/19.

The highest correlation coefficient was between Factor 1 and Axis 3 at -0.48. It is not possible to separate any particularly strong relationship between other factors and axes. The first three axes had remarkably similar correlation coefficients between all five factors, apart from the first. These other coefficients were all in the range of 0.35 to 0.39. Axis 4 correlated well only with Factor 1, while Axis 5 did not clearly correlate with any of the five factors.

This analysis of the physico-chemical factors in relation to the ordination axes was not pursued any further. At the very least, the first two ordination axes should have correlated clearly with one factor since these two axes accounted for over 28% of the total variation within the phytoplankton. But neither of the two axes had this level of correlation.

Table 6/19: Correlation of FACTORS with AXES.
Pearsons correlation coefficient n = 206.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Factor 1	-.29	-.10	-.48	-.29	.04
Factor 2	-.38	-.38	-.36	-.11	.06
Factor 3	.38	.38	.36	.10	-.06
Factor 4	.37	.39	.36	.10	-.06
Factor 5	.35	.36	.39	.13	-.07

6.4.3.2 Physico-chemical VARIABLE correlation with AXES

An alternative analysis was used to interpret the ordination axes based on the individual environmental variables.

This analysis used the same 17 variables as the above analysis (section 6.4.3.1), and the same samples, but without any preliminary data reduction by factor analysis. The individual variables were correlated with the axis loadings for the first five ordination axes, using Spearman's rank order correlation coefficient (SPSS, 1975). Rank correlation was employed so that a test of significance could be applied to each correlation coefficient without violating the associated assumptions of the test. Table 6/20 gives the correlation coefficients of each of the five axes for the 17 variables. In Figure 6/21 a visual comparison is given of each of the significant correlation coefficients on the five ordination axes. It is noticeable in this figure that pH is the most highly correlated variable with Axis 1 and that there is a diminishing degree of correlation of the variables over successive axes. Even so, several variables were still significantly correlated on Axis 5 at the 0.001 level of significance.

Variables were both positively and negatively correlated on the five axes and some variables significantly correlated with all five. Cloud cover was significantly correlated with all five at the 0.001 level. Ammoniacal nitrogen and soluble phosphorus correlated with each of the five levels at different levels of significance. Water hardness, conductivity, temperature, windrun and euphotic depth all significantly correlated with at least four of the axes.

This high degree of correlation with each of the ordination axes may explain the failure of the factor analysis correlation (section 6.4.3.1). In that analysis the variables were highly loaded on only a few of the factors (see section 4.3) and as a consequence the correlations were less significant with the physico-chemical variables. Total phosphorus correlated on only one ordination axis, and in this case the correlation coefficient was only 0.25. Rain, nitrate and total organic nitrogen were each correlated with only two axes. The correlation coefficient of nitrate with Axis 1 was 0.57, which is the highest positive correlation for any axis.

Examining the variables most highly correlated with each axis, it is possible to discover ecological implications of changes in the

Table 6/20: Correlation Coefficients of Physico-Chemical Variables with Ordination Axes

Variable	AXIS 1	AXIS 2	AXIS 3	AXIS 4	AXIS 5
Nitrate	.57***	.06	.38***	-.11	-.09
Nitrite	.10	-.19**	.23***	.17**	.03
Ammon-N	-.12*	.11*	.15*	.15*	-.15*
T.O.N.	.31***	-.07	.01	.002	-.15*
Sol-P	-.25***	.13*	.39***	-.26***	-.16**
Tot-P	.25***	-.10	-.08	.03	.002
Hardness	-.50***	-.51***	-.27***	.03	.19**
Silica	.13*	.43***	.35***	-.06	-.11
Tot-S.S.	.08	.27***	.06	-.44***	-.21**
pH	-.65***	-.22***	-.20**	.24***	-.10
Conductivity	-.46***	-.52***	-.25***	.01	.18**
Temp.	-.15*	.40***	-.50***	.24***	.03
Cloud	.38***	.28***	-.54***	-.29***	.30***
Rain	.01	.05	.30***	-.04	-.25***
Sunshine	-.10	.33***	-.42***	-.32***	.10
Windrun	.22***	.43***	-.52***	-.31***	-.007
Zeu	-.28***	-.25***	-.05	.43***	.13*

Critical values: from Conover (1980)

$$\omega_p = \frac{x_p}{\sqrt{n-1}} \quad .n = 206 \text{ at } .999 \quad \omega_p = .2158$$

$$.990 \quad \omega_p = .1624$$

$$.950 \quad \omega_p = .1146$$

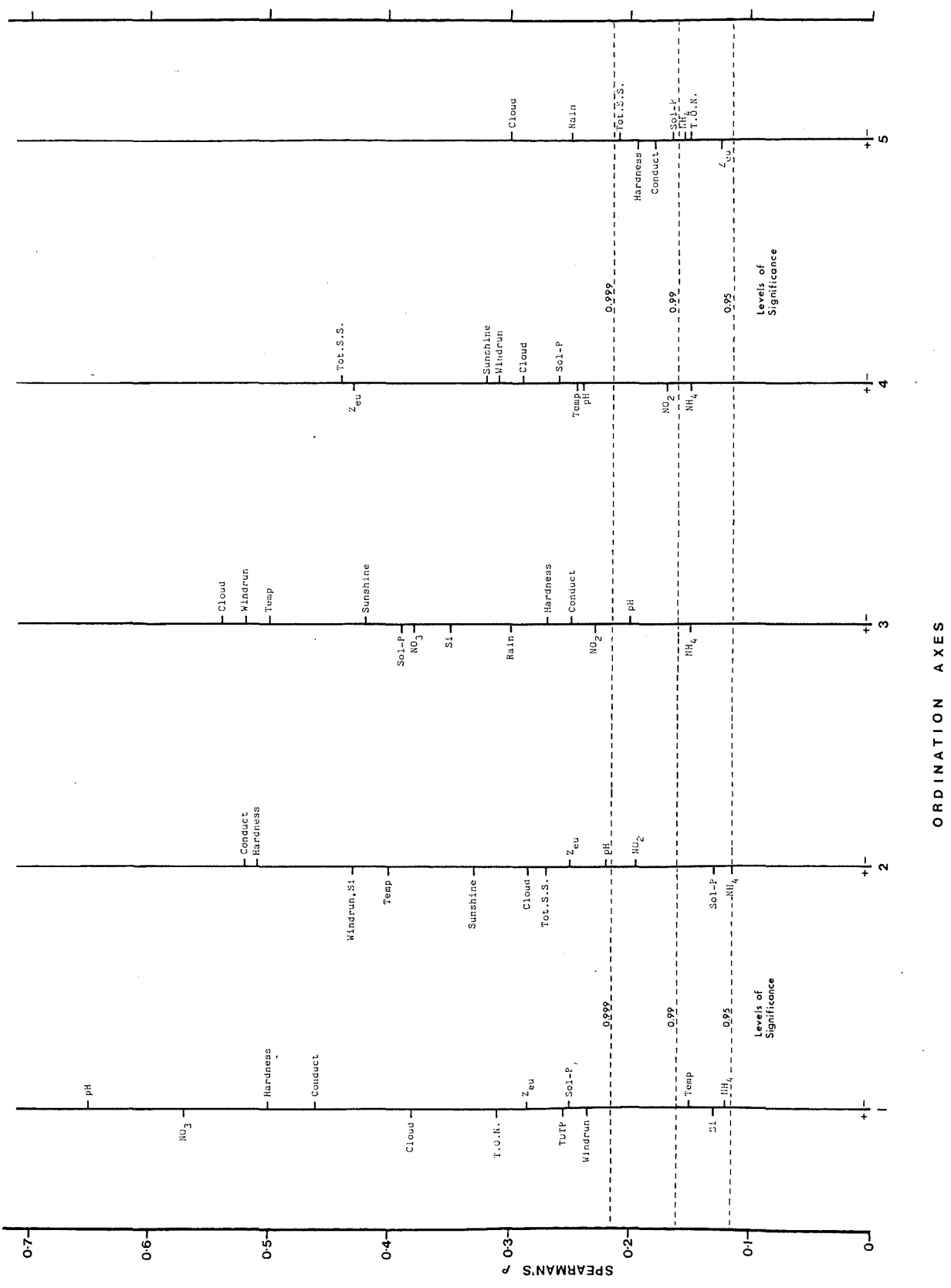


Figure 6/21: Magnitude of Spearman's Correlation Coefficients for VARIABLES on Ordination AXES, and Levels of Significance.

lake system on the phytoplankton pouplation. pH and nitrate achieved the highest level of correlation on Axis 1. These two coefficients are opposite in character. This suggests that as one variable increases, the other decreases. The river inflows were mostly high in nitrate (see section 3.2) and lower in pH than the lake; and it was a sample taken near one such inflow that was at the extreme of Axis 1 (see section 6.4.2). It must also be borne in mind that nitrate is a phytoplankton nutrient which is consumed as the population grows at the same time as pH levels increase due to the consumption of carbon dioxide. In winter nitrate might be expected to be high and pH low, while in spring and summer nitrate may be lower (depending upon supply) and pH would be higher. So there would be a shift of values down Axis 1 if results ranged from winter to summer. The extreme of Axis 1 was a sample collection in winter, August 1979, and as an earlier section has shown (section 6.4.2 and Figs. 6/17 and 6/18) the sequence of collections included an increase along Axis 1 through collections 13 and 14, and a decline with collections 15 to 17. In the same period several species of Chrysophyceae were present and fewer Diatomophyceae (see section 6.2). However it is not possible to fully interpret the sequence of all samples in these terms because of the complexity of the multiple correlations. Nitrate is plainly the most highly correlated plant nutrient and in the next section the possibility that it is the key limiting factor within the lake will be considered.

The second ordination axis correlated most significantly with conductivity and water hardness, which are related measures associated with the composition of the water. However these two variables also correlated with the first axis at a similar level, and for this reason trends in these two variables need to be related to both axes. The sample ordination plot for these axes (Fig. 6/16A) seems to suggest that the top right-hand corner should have low conductivities and the bottom left-hand corner should have high conductivities. In fact the samples collected at the period of seawater influx to the lake (see section 3.4.2.1) are found in the bottom left-hand region of the ordination plot, which is in agreement with the expected trend.

The third ordination axis negatively correlated most highly with four climate-related variables. Three plant nutrients, phosphorus,

nitrate and silica, were positively correlated at a slightly lower level. These results are in contrast to those of the first two axes where climate and nutrient variables (except nitrate) were relatively unimportant.

The fourth ordination axis was most highly correlated with total suspended solids and euphotic depth. These two variables are related to the light-regime within the lake. The fifth axis shows a relatively weak correlation with cloud cover and rainfall, two variables which had in fact been more highly correlated on earlier axes.

It is not possible to give an ecological interpretation of the ordination axes from the species ordination without experimental comparison between the individual species. These data are lacking for the present study, but it is possible to make inferences about the species if the sample ordination is carefully interpreted. By definition, the method allows for direct comparison of the axes of each ordination. For this reason, the method is alternatively called "correspondence analysis" (see introduction to section 6.4).

An earlier section (6.4.1) showed the seven taxonomic groups were distributed differently in the species ordination. It is now possible to suggest comparative ecological attributes of various species.

The Cyanophyta were only found at the low end of Axis 1, which implies they are organisms which exist in low nitrate and high pH conditions. The ability of some blue-green algae species to fix their own nitrogen allows for the ecological success of such species to compete in these conditions.

The Chlorophyceae and Diatomophyceae were positioned in the central area of the first three axes. This could imply that they were adapted best in the generally prevailing conditions of the lake, and did not prosper in extremes of conditions. However it must be borne in mind that these groups included a relatively high proportion of the phytoplankton flora, and as such must have influenced the ordination to some degree.

The Chrysophyceae spanned the full length of Axis 1, but showed a more interesting pattern in association with Axis 2. It has been suggested above that increasing conductivity would be reflected in a gradient towards the bottom left-hand corner of the Axis 1 and

Axis 2 plot. Figure 6/16A shows that Unknown sp.S60 was at this extreme corner, and therefore is probably an organism of high conductivity requirements, marine in origin. The scatter of other species probably relates to their affinities with brackish and freshwater, as suggested in an earlier chapter (section 5.6). Without careful comparative bioassay experiments it is not possible to confirm this suggestion.

Other less well represented groups included the Euglenophyceae and Cryptophyceae. They were positioned at the upper end of Axis 1 which indicates that they require low pH and high nitrate to enable them to succeed.

This discussion, based largely on the sample ordination, has shown the complexity of the phytoplankton community. This in turn has illustrated the complexity of the physico-chemical environment and lake system as a whole. The next section will discuss another aspect of this complexity, the potential limitation of phytoplankton by nutrients.

6.5 POTENTIAL LIMITING FACTORS

There is considerable documentation of the necessity for a supply of nutrients to support algal growth (reviewed by O'Kelley, 1968), but the role of nutrients in regulating phytoplankton population dynamics is much more controversial (Koonce, 1980). There has been much discussion on the relative place of carbon, phosphorus and nitrogen in limiting growth of phytoplankton in natural waters (Likens, ed. 1972).

Koonce (1980) has outlined several approaches to the subject of nutrient limitation. In this present study ratios of nutrient concentrations will be compared with the algal cellular composition ratios obtained from the literature. It is assumed that nutrient uptake is in the same proportion to the ratio of the internal composition of the cell unless one factor is limited. The ratios of nutrient concentrations can also be compared with the actual nutrient concentration to indicate depletion of the resource. Because of the untested assumptions of the method, this study is restricted to indicating 'potential nutrient limitation'. The approaches to limitation based on internal nutrient concentration of cells (e.g.

Gerloff and Skoog, 1957; Healey, 1978; Healey and Hendzel, 1980); and that of nutrient enrichment bioassays (e.g. Lund et al., 1971; Goldman, 1972; Maloney et al., 1970; Marvan et al., eds. 1979) are beyond the scope of this present study. However these other approaches would give more conclusive proof of nutrient limitation.

The present study will consider only plant nutrients, inorganic carbon, temperature and light. It is possible other minor nutrients or factors limit the population dynamics, while the major ions affect the composition of the flora, rather than the quantity of it (Talling, 1976).

6.5.1 Carbon

Carbon is the basis for organic material and as such is an essential nutrient. Since the inorganic supply of carbon is carbon dioxide from the atmosphere, it is unlikely to limit the full potential of maximum biomass, although over short periods the available supply could potentially limit the rate of photosynthesis (Westlake, 1980). Allen and Spence (1981) have shown recently that microalgae have a differential ability to utilise bicarbonate as a carbon supply, so at times of high pH when carbon dioxide is depleted (see section 4.2.5.2) bicarbonate may be available as an inorganic carbon source.

McCarthy (1980) reviewed the photosynthetic carbon fixation literature and found C:N algal composition ratios ranging from 7.5 to 20. Only if the immediate supply of inorganic carbon and inorganic nitrogen falls outside the range compatible with continued growth will the populations be potentially limited.

In this analysis the carbon supply is taken as the total inorganic carbon from both carbon dioxide and bicarbonate, as atomic-carbon. The nitrogen supply is the total inorganic nitrogen content (nitrate, nitrite and ammoniacal), but for blue-green algae elemental N can also be a nitrogen source.

Figure 6/22A includes the C:N ratio in the water over the sampling period. The maximum and minimum ratio for each sampling day are also shown. On many occasions the C:N ratio was much greater than 20 (note the log scale on the graph) which suggests potential nitrogen limitation.

On no occasion was the mean ratio for C:N in samples of lake water below the value of 7.5, but in the spring of each year the ratio fell. The minimum C:N ratio

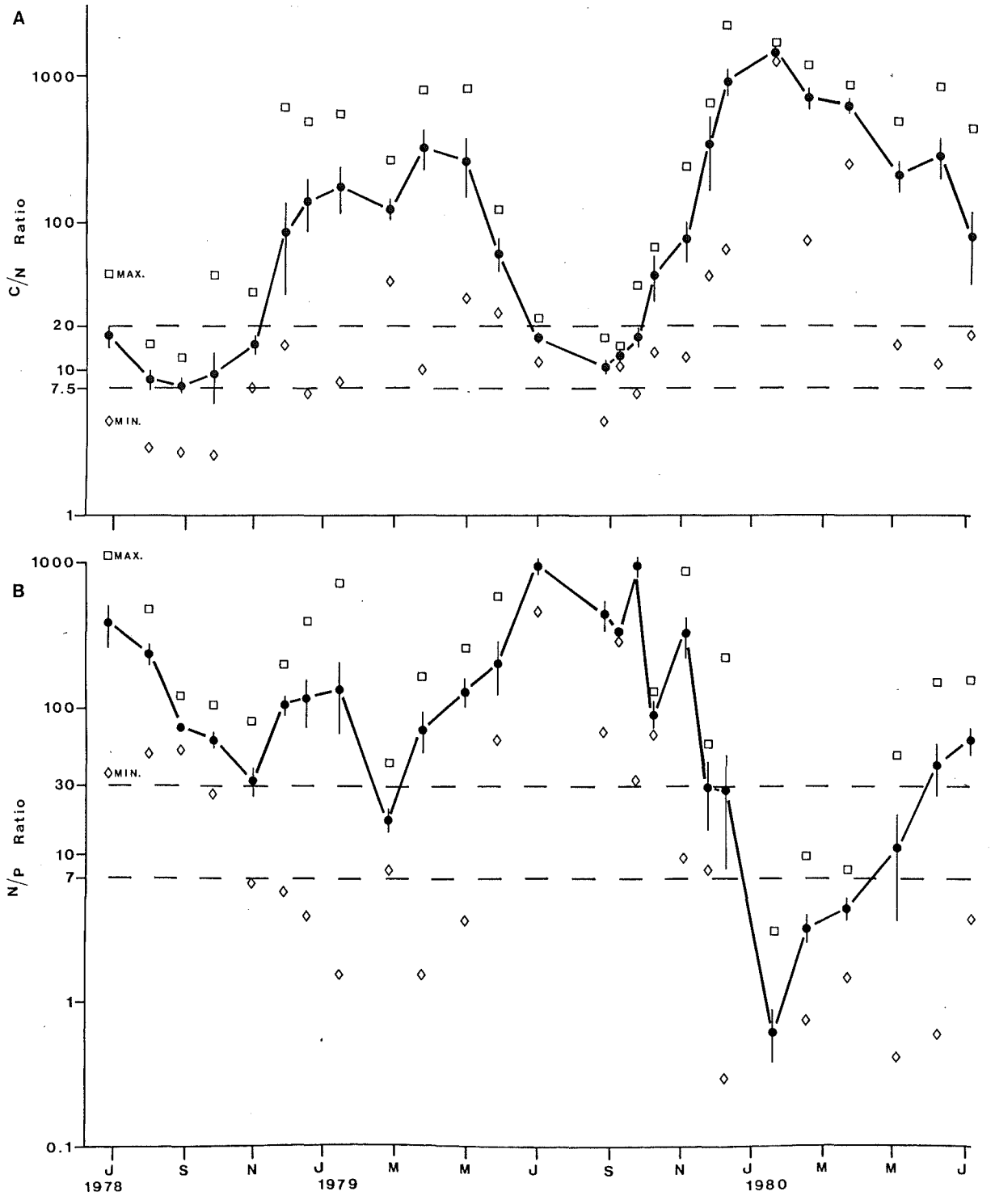


Figure 6/22: Nutrient Ratios: Mean (±S.E.), Maximum, Minimum.

A. C/N Ratio
B. N/P Ratio

shows potential limitation from July to October 1978 and during August and September 1979 for some sites.

Figure 6/23 shows the sites where the C:N ratio was less than 7.5. It is evident that low C:N ratios are associated with the inflows. Carbon limitation became widespread in 1978, for over about half of the lake the ratio was less than 7.5. During 1979 the drop in the C:N ratio was not so evident, and carbon was a potentially limiting factor only for a localized region for a short period. The lower incidence of potential carbon limitation in 1979 was related to the lower concentration of nitrogen (section 4.2.3.1) and potential nitrogen limitation (section 6.5.2) rather than a drop in inorganic concentrations.

6.5.2 Nitrogen and Phosphorus

In the previous section, periods of potential under-supply of inorganic nitrogen were noted from the C:N ratio. The more frequently used ratio is that of inorganic nitrogen with available phosphorus (N:P). Within plant cells nitrogen and phosphorus are in the ratio of 8.75:1 (Vallentyne, 1974). It has been shown experimentally that there can be a range of limitation between nitrogen and phosphorus, with a ratio range from 7 to 30, depending upon the species (Rhee and Gotham, 1980). Ratios below 7 indicate nitrogen limitation and ratios greater than 30 indicate phosphorus limitation, assuming there is no other limiting factor. The difference between the N:P ratio within the cells and that of the experimental uptake may be due to surplus uptake of phosphorus (Fitzgerald and Nelson, 1966).

The forms of inorganic nitrogen generally available to phytoplankton are nitrate and ammonia (Brezonik, 1972) although recent work shows utilization of nitrite (Latorella et al., 1981). The phosphorus form immediately available for uptake by phytoplankton is soluble phosphorus.

The N:P ratio available for algal uptake has been calculated from the total inorganic nitrogen and the soluble phosphorus concentrations in water samples. Over the two year period (251 samples) the range of ratios found was 0.045 to 1855. Figure 6/22B shows the mean N:P ratio and also the maximum and minimum for each sampling day.

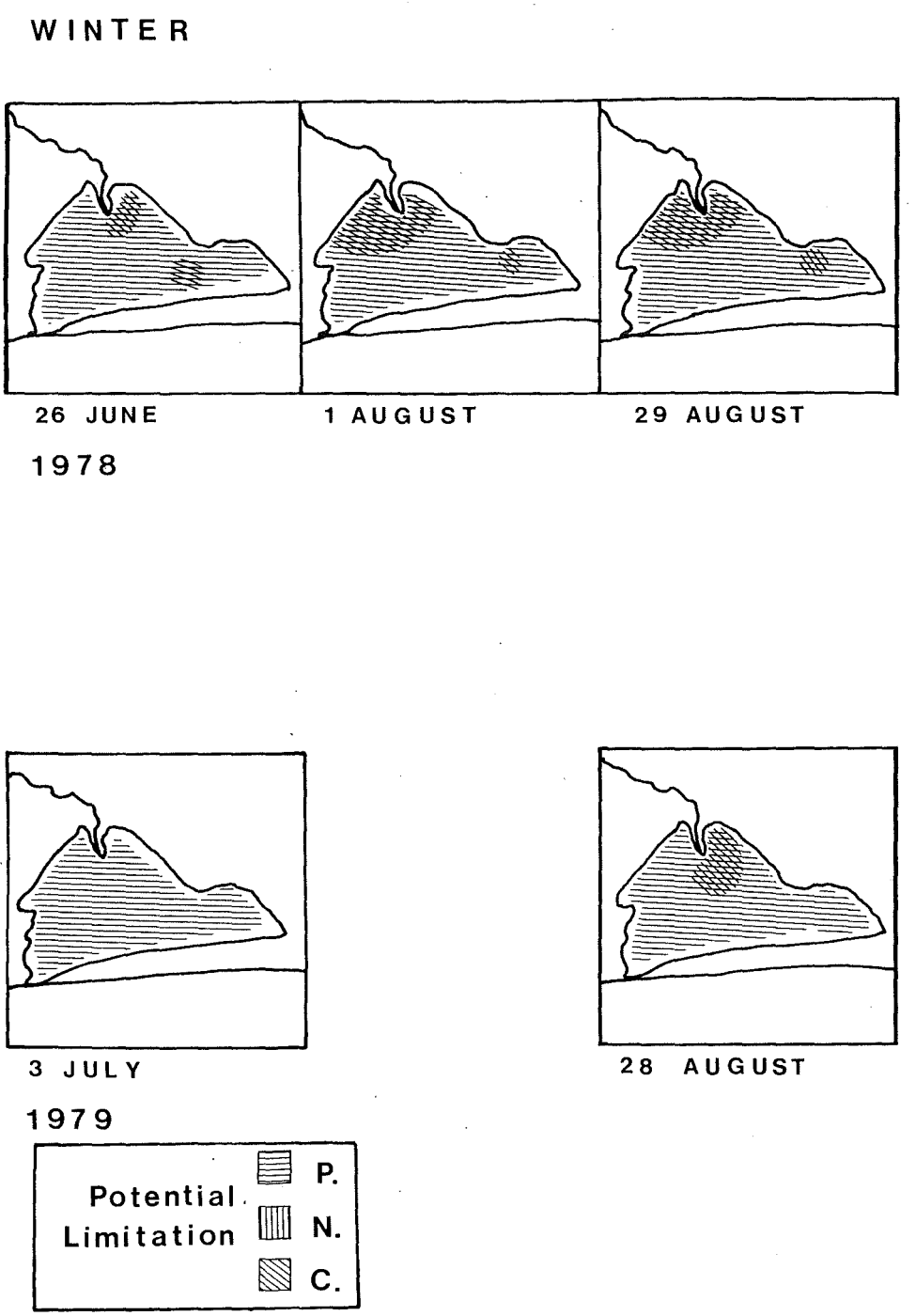


Figure 6/23: Potential Nutrient Limitation. - Winter.

A one-page copy of this figure is given as Supplementary Figure 6.

SPRING

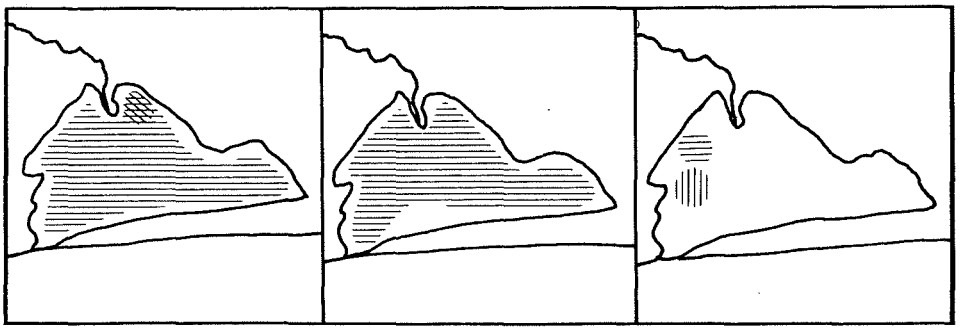


Figure 6/23 continued.

Potential Nutrient Limitation - Spring.

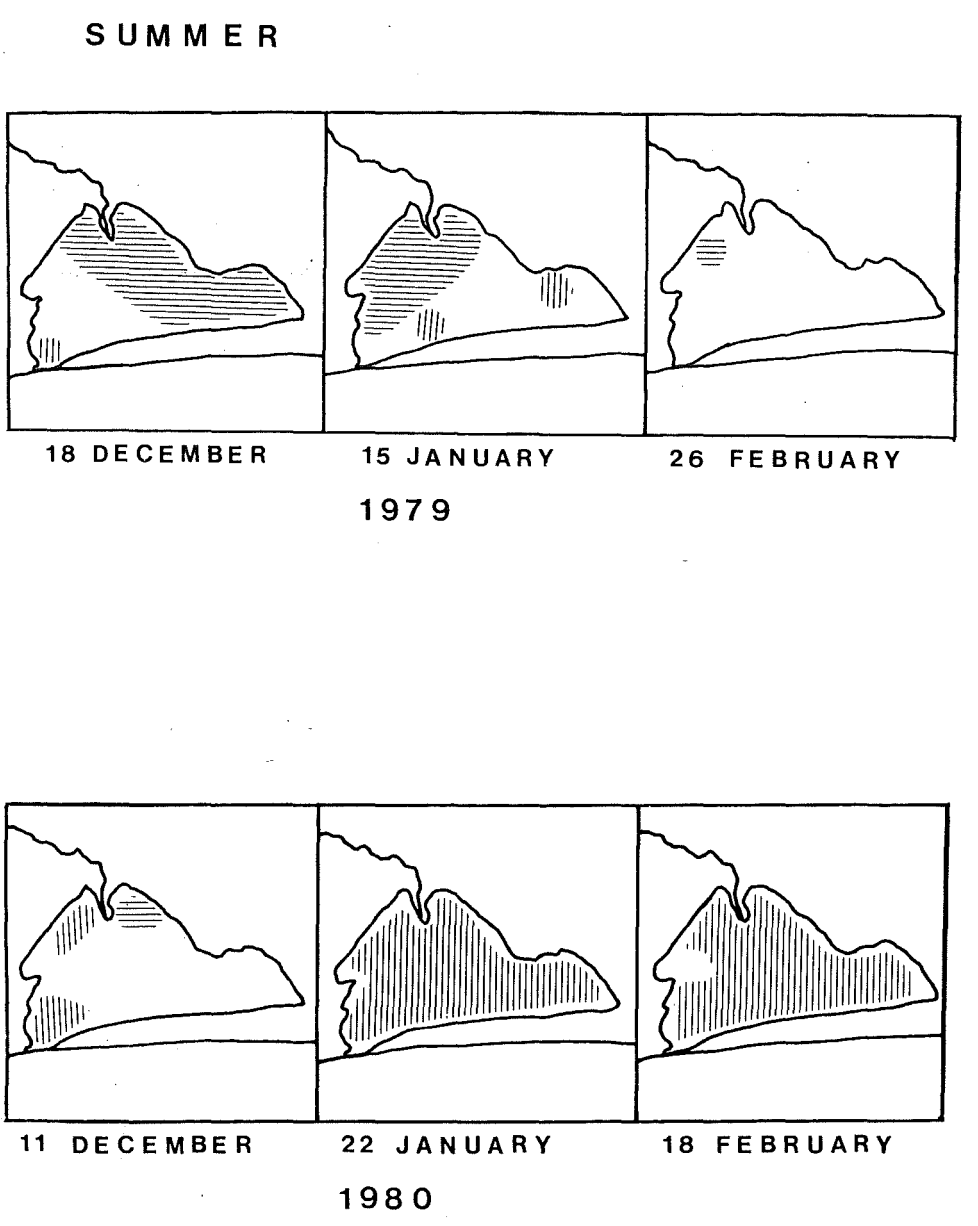
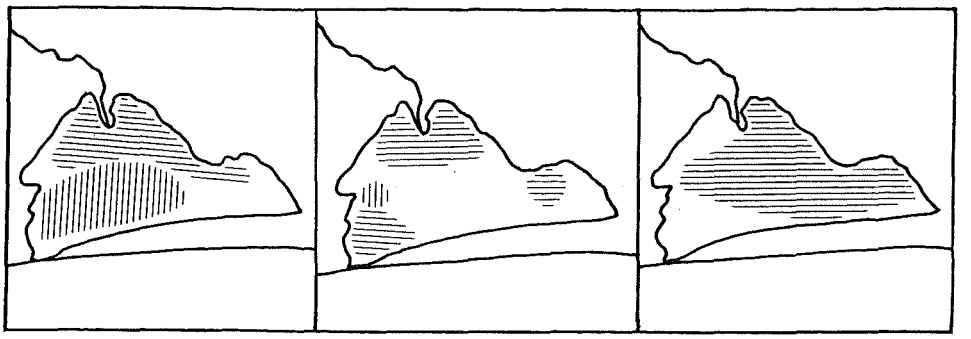


Figure 6/23 continued.

Potential Nutrient Limitation - Summer.

AUTUMN



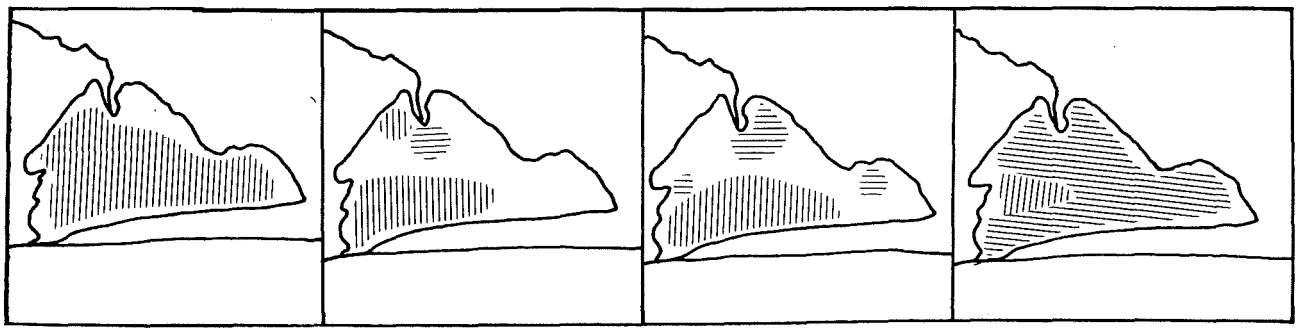


Figure 6/23 continued.

Potential Nutrient Limitation - Autumn.

Potential nitrogen limitation was found for some sites in both summers. In the first summer, 1978-1979, nitrogen limitation only occurred at a few sites. The mean ratio for the lake did not fall below 17.5 over this period. In the second summer, 1979-1980, nitrogen limitation was more severe, with several sites being nitrogen limited from December to July. The mean for the whole lake indicated potential limitation from January to March.

The suggestion of potential nitrogen limitation is confirmed by the concentrations of inorganic nitrogen (Section 4.2.3.1). During the summer period the inorganic nitrogen concentration fell to its lowest recorded levels. In the summer of 1978-1979 the decline of nitrogen levels was not as severe as in the following year. In January 1979, 9 of the 11 sites had less than 0.02 $g.m^{-3}$ of nitrate nitrogen for one month; and in the following year most sites had less than 0.02 $g.m^{-3}$ for more than four months. During January 1980 in particular, all sites had less than the minimum detectable level of 0.001 $g.m^{-3}$ nitrate nitrogen.

High values in the N:P ratio indicate potential phosphorus limitation provided other factors are in surplus supply. These periods occurred during the winter of each year, and also for some sites in the summer 1978-1979 (Figure 6/22B). The highest N:P ratio of 1855 was found in September 1979, at a site which was also potentially carbon limited.

Nutrient limitation is rarely used to explain the limitation of the population in winter for the majority of lakes which have been studied. Most lakes studied have been in continental locations and subject to more extreme temperature changes in winter than is Lake Ellesmere. The effect of this is for temperature and light to severely limit these lakes through the formation of surface ice. For Lake Ellesmere this does not occur and it is possible therefore that nutrient limitation may occur in winter periods. It appears that phosphorus is potentially limiting at these times.

The case for potential phosphorus limitation in summer is clearer. In the summer of 1978-79, a period in which it has already been noted there were small regions of nitrogen limitation, there are other larger regions where the high N:P ratio indicates phosphorus limitation.

Figure 6/23 shows the sequence of potential nitrogen and phosphorus limitation, superimposed on the potential carbon limitation

pattern. Potential phosphorus limitation was important at many sites in the period June 1978 to November 1979. At the same time, small areas of nitrogen limitation were present. From December 1979 to June 1980 potential nitrogen limitation was common, but after that phosphorus limitation again predominated. All the areas of potential carbon limitation (except October 1978, Site 13) coincide with potential phosphorus limitation.

Comparison of the soluble phosphorus concentrations (section 4.2.3.2) with those of carbon suggests the greater likelihood that carbon was the limiting factor. During the period July to September 1978 the soluble phosphorus concentration was the highest of the whole two year period. This suggests that carbon was limiting the population growth and that phosphorus was in surplus supply. Once carbon was no longer limiting, the phosphorus concentrations fell quickly. From May to July 1979 the phosphorus concentrations were at a minimum and phosphorus limitation occurred throughout the lake. In August and September 1979, carbon was again a limiting factor and the phosphorus levels rose, only to decrease in early November. From November 1979 to July 1980 soluble phosphorus concentrations were higher, and this coincided with a period of severe nitrogen limitation.

6.5.3 Silica

Lund (1950) has shown for Windermere that silica does not become limiting for Asterionella until it is depleted to less than 0.5 $g.m^{-3}$. Similar concentrations have been found for other diatom genera (Golterman, 1975a).

The silica concentration in Lake Ellesmere rarely falls below 7 $g.m^{-3}$, and samples which did fall below this level were associated with seawater influx (see Section 4.2.3.3). The minimum recorded level was 1.3 $g.m^{-3}$ in Collection 20.

On this account silica is unlikely to be a limiting factor within Lake Ellesmere.

6.5.4 Temperature

Moss (1973b) and Carpenter (1973) have shown the importance of temperature in regulating phytoplankton populations. Moss found little growth in a range of phytoplankton species below a temperature

of 4°C, or above 35°C. The optimum growth occurred at 21.4°C. Carpenter found similar results for brackish water organisms.

As reported previously (section 4.2.6.1) the day temperatures for Lake Ellesmere are within this acceptable range. Unlike many other temperate lakes, Lake Ellesmere does not freeze during the winter although the minimum temperature approaches 0°C. Winter temperatures may therefore slow growth, but they do not stop it. Extreme summer temperatures are also unlikely to be high enough to have a serious effect.

The factor of evaporation is, however, important for a shallow lake during summer. Evaporation tends to concentrate the major ions and other nutrients. Moreover, evaporation in summer lessens the pressure to open the lake, especially after any opening during the late spring period. It has been difficult from this present study to give data to support this contention, other than the higher mean salinity in the shallow embayment near the Selwyn River mouth (see section 4.2.1).

6.5.5 Light

Talling (1971) has discussed the three components which determine the underwater light climate in lakes. He considered the important factors to be the surface incident radiation, the relative penetration of light within water and the proportions of illuminated and "dark" water within the mixed water column. Wind is another factor, and Herodek and Tamás (1975) have suggested that wave formation due to wind affects the illumination of deep levels in turbid waters.

Lake Ellesmere has already been discussed in terms of light penetration (section 4.2.6.2), where it was shown that minimal light penetrated to any depth in the lake.

The two forms of light limitation in a water body are "surface inhibition" due to high incident light, and limitation due to cells being out of the euphotic zone for long periods (Talling, 1971). Surface inhibition is a controversial matter. It is more likely to occur in places where the light has a high intensity. Tilzer (1980) suggests that irradiance greater than

60% of surface level around noon may be inhibitory, but there is some evidence that it may also occur in shallow Antarctic lakes (Goldman et al., 1963).

Probably more emphasis should be given to light limitations when cells are out of the euphotic zone for long periods of time. This occurs when the depth of the mixed layer exceeds the depth of the euphotic zone. In deep lakes, this occurs during isothermal mixing, and in very densely populated waters it is caused by self-shading. Talling (1971) suggests this can occur in rivers which flow slowly, as found by Javornický (1966).

Depth profiles of production would be needed to demonstrate that Lake Ellesmere is light limited. However, there is reason to expect that the very shallow euphotic depth implies potential light limitation. It is not possible to isolate the self-shading effect of the phytoplankton from that due to non-algal sediment, which was shown to be a significant factor in the water column (section 4.2.6.2). Wind is the cause of this sediment disturbance, but wind also contributes to the continued movement of algal cells towards the surface light.

This discussion of potential limiting factors within Lake Ellesmere can be related back to the community structure of the phytoplankton flora (section 6.4) in order to make predictions of possible changes in floral composition under different lake regimes. The most important factor in this respect is nitrate nitrogen. It has been suggested that this nutrient is potentially limiting over wide areas of the lake for long periods, especially during summer 1980. Using the interpretation of the ordination axes based on the correspondence between sample and species ordinations (section 6.4.3), different species were interpreted according to ecological requirement. From that analysis, the Cyanophyta were identified as having a low nitrate requirement, whereas Euglenophyceae and Cryptophyceae occurred under high nitrate conditions. On this basis, a shift in the floral composition towards blue-green algae might be expected when nitrogen limitation is most severe. The consequences of such a shift has an important implication in terms of the quality of the lakewater, since amongst the blue-green flora is the toxic alga Nodularia spumigena.

The effect of the other potential limiting factors is not as easily interpreted. The reason is that they were not highly correlated on the ordination axes. Factors such as conductivity and water hardness were important in the ecological interpretation of the ordination, but were not considered as limiting factors within the lake. It is not possible to make more definite predictions of changes in the floral composition of the lake without supporting experimental data.

CHAPTER 7

DISCUSSION

The previous four chapters have detailed the physical, chemical and floral aspects of the ecology of Lake Ellesmere. A number of unique features were highlighted throughout the previous discussion. This present chapter will consider some of these features and compare them with others mentioned in studies from New Zealand and overseas.

The features to be discussed in detail are the location of the lake, the influence of climatic features, the nutrient regime and trophic status, and the phytoplankton flora.

7.1 SIGNIFICANCE OF LOCATION

Lake Ellesmere is the fourth largest lake in New Zealand, and its extreme shallowness and location on the edge of a rich agricultural plain has a great influence upon it. The largest lake is Lake Taupo in the central North Island which is 6161 sq. km and 163 m maximum depth, and is volcanic in origin. Lakes Te Anau and Wakatipu in the southern half of the South Island are next largest. These lakes are of glacial origin and range in depth from 380 to 417 m (Irwin, 1975). The origin and location of Lake Ellesmere is markedly different from these larger lakes. These features also have an important bearing on the trophic status of the lake, as will be discussed in a later section (7.3). It is pertinent to note at this point that these three larger lakes are all considered to be oligotrophic (Flint, 1975; White and Downes, 1977).

The area around Lake Ellesmere is flat (except for Banks Peninsula to the east), and numerous drains and rivers enter the lake from the large surrounding agricultural area. These inflows are particularly important as sources of nutrients. Although no attempt was made in this study to identify the sources of particular nutrients, the main activites within the catchment are arable and pastoral agriculture (Hughes et al., 1974). Point sources of nutrients include the effluent discharge from the Lincoln sewage works into the LII River, and the Leeston sewage works to the Leeston Drain. No

industrial activity is known to make a significant contribution to the inflows into the lake. Domestic effluent disposal by means of septic tanks provides many other small point sources of nutrients. This disposal method contributes to the groundwater of the area, in addition to the non-point sources due to agriculture. Although no direct flow of groundwater into Lake Ellesmere has been established to date (see section 3.1), the quality of the groundwater has an influence on the surface drainage system of the area. It was noted (section 3.1.2.2) that the spring-fed Hart's Creek and Halswell River had high concentrations of inorganic nitrogen, and the Halswell River had high phosphorus concentrations.

The importance of agricultural influences on lakes has often been recognised within New Zealand. White (1982) emphasized the location of lakes within New Zealand, and noted that the lowland lakes are mostly eutrophic, whereas the highland lakes of the South Island are almost all oligotrophic. The exceptions were Lakes Hayes and Johnson, the catchments of which are largely pastoral. O'Connor (1968), McColl and Hughes (1981), and McColl (1982) all discuss the effect of land use with catchment areas on the water quality of lakes. McColl noted that greater emphasis had recently been placed on the control of point sources of agricultural waste, such as dairy-shed and piggery effluents. However there has been a corresponding neglect of the significance of non-point disposal sources, such as spray irrigation and lagoon treatment. A similar concern was expressed overseas in a study by Bachmann (1980), in which point sources of nutrients were removed in order to reverse eutrophication, but as a consequence, non-point sources assumed greater importance. Khaleel et al. (1980) found that nitrogen and phosphorus concentrations in runoff water from agricultural land correlated in a highly significant manner with the loading applied to the land initially. This suggests that fertilizers are an important non-point nutrient source in some areas. Gasser (1980) and Oakes et al. (1981) have analysed the effect of agricultural practices especially in relation to groundwater and runoff. Although the spatial distribution of nitrogen depends on the geometry of the aquifers, higher levels are usually found in areas of arable farming, whereas phosphorus is generally retained in the soil and does not move into drainage water or deep aquifers. Within the

Ellesmere area, Adams et al. (1979) have recorded a similar result.

A further nutrient source which might affect Lake Ellesmere is that derived from aquatic birds. Although not assessed in this present study, it may be of considerable importance due to the high bird populations recorded in the vicinity of the lake. Populations of black swan (Cygnus atratus) as high as 80,000 have been recorded (Hughes et al., 1974), as well as many other species. Brezonik (1972) found that a small Florida lake had nutrient loading rates well beyond the accepted critical levels, due to the presence of a community of 50 mallard ducks (Anas platyrhynchos). Brinkhurst and Walsh (1967) considered that Rostherne mere was eutrophic as a result of the faeces of a gull population which roosted and over-wintered on the lake. No data are available on the composition of faeces of the birds commonly found on Lake Ellesmere, but this might be considered an important nutrient source. The distinction should be made, however, between those birds which feed within the lake (cycling nutrients) and those feeding beyond the lake (adding nutrients).

One significant feature of Lake Ellesmere is its shallowness, which aids the resuspension of solids within the water column (see section 4.2.6.2). Within New Zealand this feature is difficult to compare because the other large lakes are all extremely deep. Sediment suspension and water movement are unlikely to cause the same degree of turbidity in deeper lakes. Internationally, large shallow lakes have been the subject of specialist ecological symposia (Salanki and Ponyi, eds. 1975; Dokulil et al., eds. 1980). The better known shallow lakes which have been investigated include Neusiedlersee (Löffler, ed. 1979), Loch Leven (Bailey-Watts, 1982) and Lake Balaton (Herodek and Tamás, 1975). Many small shallow lakes have also been studied intensively, including those in Australia (Gordon et al. 1981), North America (Haertel, 1976; Hickman, 1979a,b), Sweden (Willén, 1977) and Iceland (Jonasson and Adalsteinsson, 1979). The features which Lake Ellesmere shares with these lakes include shallowness, eutrophic state and non-stratification. Lake Ellesmere's soft bottom and consequent turbidity is like that of South Bay in Texas. Copeland (1974) found South Bay's shallow impoundment to be particularly turbid because of the wind action. Banks (1975) described this wind action on shallow lakes within a mathematical model of the system, and Murphy (1962) found that

high turbidity reduced the productivity of a lake because of the restriction of energy available for photosynthesis.

The final significant feature of the location of Lake Ellesmere is its close proximity of the sea. A direct consequence is the influx of seawater which causes the brackishness of the lake (see section 4.2.1). The barrier which separates the lake from the sea is obviously very significant. Without such a barrier, Lake Ellesmere would probably be a tidal estuary similar to that on the northern side of Banks Peninsula, the Avon-Heathcote Estuary. The active movement of gravel up the Canterbury Bight (Armon, 1974; see section 1.2) maintains this barrier, and is also responsible for closing the lake off from the sea after it has been mechanically opened. There are several other lakes of this type around the New Zealand coast. Irwin (1975) identifies these lakes as "bar types", and lists 18 around the South Island. Most of them are small (less than 0.5 sq. km), but Tomakawk lagoon near Dunedin, Washdyke lagoon near Timaru, Lake Forsyth adjacent to Lake Ellesmere and Lake Grassmere in Marlborough are rather larger. In the North Island there are several "bar type" lagoons near Wairoa, and Lakes Onoke, Kohangapiripiri and Kohangatera near Wellington. The coastal dune lakes on the west coast of the North Island are essentially different in origin, in being shallow basins formed by wind-blown sand (Irwin, 1975). Cassie and Freeman (1980) have done a detailed comparison of a series of these dune lakes.

The water quality of true "bar type" lakes has not been studied in detail. Mason's study (1950) of Lake Kohangapiripiri and its vegetation is the result of one visit, and Lake Onoke has only been discussed in terms of foreshore protection (King, 1972), so little is known about the lake itself. In the South Island, Lake Grassmere is highly modified, being periodically flooded and evaporated for commercial salt production. Washdyke lagoon has been investigated with respect to its use for wastewater treatment by Steven, Fitzmaurice and Partners (1981). They noted occasional algal blooms in the lagoon. Two other lakes have been studied in greater detail. The phytoplankton productivity, macrophyte production and environmental factors of Tomahawk lagoon were studied over a three-year period (Mitchell, 1971). It has obvious similarities with Lake Ellesmere, since both lakes are near the sea and this shows up in the brackish

nature of the water of both lakes. Although using productivity, rather than standing crop, as in this study, Mitchell found phytoplankton was inversely related to the visibility of the water. Furthermore phytoplankton and macrophytes alternately dominated the lagoon in an irregular cycle.

Lake Forsyth is adjacent to Lake Ellesmere and as one might expect it is similar in many respects. Forsyth normally has no outlet, but is opened to the sea once every few years. It is brackish, shallow and eutrophic (Burnet and Wallace, 1973). The flora of Forsyth is dominated by blue-green and green algae and is similar in composition to that of Lake Ellesmere (Flint, 1975). Particularly important in Forsyth is Nodularia spumigena, which has caused water blooms in the lake over many years (McCaskill and Flint, 1970; Flint, 1975).

7.2 SIGNIFICANCE OF CLIMATIC FEATURES

The importance of wind in relation to the depth of the lake has already been discussed above. This section will consider the frequency and occurrence of wind as a climatic feature, along with the temperature and rainfall regimes found at Lake Ellesmere, and their significance in the functioning of the lake as a system.

The wind on Lake Ellesmere produces a suspension of sediment and mixing of water as has already been noted. The frequency and occurrence of the wind regime of the area therefore requires analysis. In section 3.3 wind was described as an important feature of the Canterbury climate due to the westerly wind system and the features of the Southern Alps. Stout (1969) noted the way wind caused the mixing of lakewater in several high country lakes in Canterbury. She attributed the poor development of thermoclines even in relatively deep lakes to this factor.

Wind is also known to be important in the maintenance of phytoplankton within the water column. George and Heaney (1978) found that wind was a factor influencing the spatial distribution of the plankton in Estwaite Water. Therriault and Platt (1981) recorded a similar result for a coastal embayment. Periods of low turbulent mixing were reflected in taxonomic or physiological differences within the population, whereas at times of high winds

there was a damping effect of spatial variations. This may help to explain why the phytoplankton standing crop over wide areas of Lake Ellesmere has common characteristics. The same species, with similar population sizes, were found over wide areas of the lake. Variation occurred relative to time rather than to spatial distribution.

Marins (1981) found that the wind action was important in maintaining Melosira italica within the water column of a reservoir in Brazil. He emphasized that wind must be considered in phytoplankton ecology. It is notable in this regard that the flora of Lake Ellesmere was dominated by non-flagellated organisms and that the euphotic zone was frequently very shallow (section 4.2.6.2). The importance of wind in maintaining the phytoplankton within the euphotic zone should not be under-estimated.

The temperature regime of the Ellesmere district and its influence upon the lake is an important component of the lake system (See sections 3.3.2 and 4.2.6.1). This is undoubtedly moderated by marine influence. Unlike many continental temperate lakes, Ellesmere is subject neither to freezing in the winter nor thermal stratification in the summer. The lack of a winter freeze should not be neglected since it is very important in many lakes. The concept of winter and spring 'overturn' in relation to nutrient concentrations in lakes (see section 1.1) has in fact most frequently been applied to lakes subject to low temperatures and little growth during the winter. The melting of ice in the spring causes the nutrient-rich hypolimnial waters to mix with nutrient-poor epilimnial waters (Moss, 1980). Freezing is thus the basis of the idea of 'overturn' and Vollenweider's (1971) concept of nutrient concentrations associated with different trophic states (see section 4.2.8). For Lake Ellesmere this concept of 'overturn' concentrations is therefore misleading. Although higher winter concentrations of nitrate were found, no significant accumulation of phosphorus was observed. The use of nutrient concentrations to determine trophic states, based on the spring acceleration of growth, seems quite inappropriate. Consequently the mean yearly concentrations of nitrogen and phosphorus were also considered in assessing trophic status (section 4.2.8).

Temperature can be an important factor in succession of species. Flint (1938) in her early work on Lake Sarah found that temperature was

an important factor for seasonality amongst the plankton. Hammer (1964) also demonstrated that water temperature was one factor which influenced the timing of bloom formation in blue-green algae. In Lake Ellesmere the sequence of dominant organisms was different in each year studied (section 6.3.1). Some of these changes might be related to the changes in temperature between the two years. December 1979 was on average distinctly warmer than the expected normal temperature (section 3.3.2), and the algal blooms were significantly greater in this period.

Rainfall is difficult to assess as a climatic feature influencing Lake Ellesmere. Although not generally given much importance as a direct factor within a lake system, it is different in the case of Lake Ellesmere. It was shown (section 3.1.1) that on an annual basis the rainfall that falls directly into the lake is a significant amount. This rainfall however occurs only sporadically (section 3.3.1). Although no analyses of rainfall have been carried out, it must dilute the lakewater of both nutrients and salinity. Rainfall also indirectly influenced the phosphorus content of the lake. The phosphorus concentration of the inflow rivers was found to be related to the rainfall over the previous month (section 4.2.3.2). Rainfall is therefore a climatic factor of some importance within the lake system.

7.3 TROPHIC STATE INDICATORS

Lake Ellesmere has been described as highly eutrophic to polytrophic (section 4.2.8). This description is based on the definition of eutrophication in terms of the plant nutrients, nitrogen and phosphorus as set out in section 1.1. The other indirect measures used in this study, total cell numbers and biovolume, give support to this designation (section 6.3).

Burnet and Wallace (1973) have used productivity measurements to show that Lake Ellesmere is in an eutrophic state. However the tabulated nutrient data for nitrate they recorded is considerably lower than the mean found in this present study. Hughes et al. (1974) also tabulated the available nutrient data, eight samples from 1965 to 1972, and concluded that the lake was "fairly nutrient rich" (1974: 8) in the meso- to eutrophic range with regard to phosphorus, and with considerably higher nitrate levels than the Rotorua lakes. The results

of the survey conducted in 1973-1974 have also been compared with the present study (section 4.2.3). The nitrate levels were much lower than those in 1978-1980; whereas the phosphorus levels were about the same although considerably greater than given by Burnet and Wallace (1973) and Hughes et al. (1974). On this basis it is tempting to speculate on the advancing eutrophication of Lake Ellesmere. However this argument is problematic. The total range of nitrate nitrogen concentrations found in Lake Ellesmere during 1978-1980 was 0.01 to 3.75 $g.m^{-3}$, and this range covers all previous records. It is therefore possible that a limited number of samples could produce a spurious result. Likewise the full range of total phosphorus recorded in the present study incorporates the range tabulated by Hughes et al. (1974). Phosphorus is also difficult to compare because of the change in methods of analysis over time (Chemistry Division, D.S.I.R., pers. comm.). However the general thesis of increasing eutrophication remains probable.

A comparison of the nutrient content of Lake Ellesmere and other New Zealand lakes is difficult. White (1982) in a general survey of lakes emphasized the generally low nutrient content of New Zealand lakes compared with those of Europe and North America. This is supported in the work of Jolly (1968), McColl (1975), and Mitchell and Burns (1981) for a widespread number of lakes. Ammoniacal nitrogen levels were often greater than nitrate nitrogen levels in these lakes. Examples of such lakes are Rotoehu, Rotorua, Ngahewa, Ngapouri, Okaro and Rotowhero in the North Island (McColl, 1975); and Lake Hayes and Johnson in the South Island, at some times of the year (Mitchell and Burns, 1981). Mitchell (1971) found Tomahawk lagoon to have no detectable nitrate nitrogen (0.08 $g.m^{-3}$) and minimal ammoniacal nitrogen (0.003 $g.m^{-3}$). Stout (1975) on the other hand found that two coastal lakes near Kaikoura, Rotoiti and Rotorua, had very high nitrate nitrogen levels, up to 2.0 $g.m^{-3}$. Lake Ellesmere is therefore similar to these lakes with respect to nitrate, but not with regard to ammoniacal nitrogen. The Kaikoura lakes ranged up to 1.57 $g.m^{-3}$ in ammoniacal nitrogen, whereas Ellesmere ranged up to only 0.16 $g.m^{-3}$. White (1982) also considers total nitrogen concentration in relation to trophic status and shows Lake Horowhenua as having the highest level (in a restricted list of lakes). Lake Horowhenua had a total nitrogen content of 1.3 $g.m^{-3}$, whereas Lake Ellesmere has a mean of greater than 1.6 $g.m^{-3}$, and range up to 4.4 $g.m^{-3}$. This level is

comparable to that quoted by White (1982) for an OECD programme overseas.

Phosphorus is more difficult to assess because of the uncertain nature of the fraction analyzed in different studies. Stout (1975) in a comparison of lakes in Canterbury, Westland and Nelson gave ranges for total phosphorus up to 1.0 $g.m^{-3}$ for large coastal lakes (Ellesmere and Forsyth). This level is comparable to the maximum level recorded in this present study (section 4.2.3.2). The other lakes in the area had considerably lower total phosphorus levels. The eutrophic Kaikoura lakes had concentrations ranging up to only 0.295 $g.m^{-3}$ (Stout, 1975). McColl (1975) gives the concentrations of total phosphorus for a range of thermal and cold water lakes of the Volcanic Plateau. Lake Ngahewa had the highest concentration at 0.182 $g.m^{-3}$. Neither Mitchell (1971) nor Mitchell and Burns (1981) included total phosphorus measures in their studies of eutrophic South Island lakes. However White (1982) includes this parameter for a range of lakes, of which Horowhenua had the highest concentration at 0.501 $g.m^{-3}$, Rotongaio had 0.231 $g.m.^{-3}$ total phosphorus. Both of these values are considerably higher than the mean value given for Lake Ellesmere in this present study (0.151 $g.m^{-3}$). Currie (1978), commenting on the trophic status of Lake Horowhenua, pointed out that treated sewage from the Borough of Levin contributed 80% of the phosphorus input to that lake, while another 13% came from cowsheds and piggeries.

It is evident that Lake Ellesmere is unusual when compared with most other New Zealand lakes with regard to nutrient status. This may just reflect the limited number of lakes studied. Only the Kaikoura lakes, Rotoiti and Rotorua were in any way comparable to Ellesmere's concentration of nitrate. At least three lakes are known to have higher concentrations of total phosphorus: Lakes Horowhenua, Rotongaio and Ngahewa. Considering the definition of eutrophication (section 1.1), the term polytrophic should be applied to these lakes as well.

The use of mass-flow analysis made possible a ready comparison of inputs of nutrients into Lake Ellesmere (section 3.1.2.2). The nitrogen input from the rivers is largely in the form of nitrate, with little contribution from nitrite or ammoniacal nitrogen. This is somewhat different from Lake Rotorua, where Fish (1975) found ammoniacal nitrogen provided nearly twice the nitrogen input that nitrate did. Compared on the same time basis, Lake Ellesmere has a mass-flow

rate for nitrogen much greater than that for Lake Rotorua. (Ellesmere tot-N = 57.76 $g.s^{-1}$; Rotorua NO_3-N + NH_4 - N = 8.06 $g.s^{-1}$). The phosphorus input to Rotorua, however, is much greater than for Lake Ellsemere (Ellesmere sol-P = 0.327 $g.s^{-1}$; Rotorua PO_4-P = 1.076 $g.s^{-1}$). The differences between these two lakes must be related to the source of the inputs. Lake Rotorua has a major sewage component which supplies 13% of the phosphorus input (Fish, 1975), whereas Ellesmere's input is largely from an agricultural area with high nitrate levels.

Further comparison is possible with Lake Rotorua when considering specific nutrient loadings. It was shown earlier (section 4.2.7) that the specific nutrient loadings for Lake Ellesmere were above Vollenweider's critical levels for both nitrogen and total phosphorus. White (1977) calculated annual surface loadings for Lake Rotorua and found loadings for nitrogen of 3.1 $g.m^{-2}.yr^{-1}$ and for phosphorus of 0.43 $g.m^{-2}.yr^{-1}$. This phosphorus loading is twice that of Lake Ellesmere, but the nitrogen level is somewhat lower. It must be borne in mind that Lake Rotorua is a deeper lake (mean depth 10.68 m; White, 1977) so that the specific surface loadings are closer to the significant critical values as given by Vollenweider. Currie (1978) calculated the phosphorus loading of Lake Horowhenua as 3.4 $g.m^{-2}.yr^{-1}$. In this case, the mean lake depth is comparable to Ellesmere, and so this specific loading is significantly greater. Undoubtedly this is due to the input of domestic sewage into the lake.

It is also possible to compare Lake Ellesmere with other New Zealand lakes on the basis of indirect indices of eutrophication, namely total cell numbers and total cell biovolume. Cassie (1969) included total cell numbers of surface phytoplankton in a study of Rotorua. The maximum cell concentration there was 5 x 10^3 cells per ml for open water in March 1967. Burns and Mitchell (1974) recorded a maximum standing crop for Lake Hayes of 65,000 cells per ml in December 1971. For Lake Johnson the maximum standing crop in December 1970 was 117,600 cells per ml during an Anabaena bloom. For both Lakes Hayes and Johnson the standing crop was greater in summer than in winter. Cassie (1978) included maximum cell counts for the four lakes in the Rotorua district. Lake Rotoehu had a maxima less than 1 x 10^3 cells per ml. When these other studies are compared to this study, Lake Ellesmere's records indicate a greater standing crop. The maximum standing crop was

5.9×10^6 cells per ml, with a mean over the whole lake at this time of 4.7×10^6 cells per ml (section 6.3). This occurred during May 1980. It is notable that this peak in standing crop, expressed as cell numbers was in autumn; whereas for other lakes the maximum was in summer, usually February.

The use of cell numbers on a water volume basis has been used in the past to quantify a water-bloom. The phenomenon of water-bloom or 'breaking of the mere' has already been discussed in connection with Ellesmere Mere in Shropshire (section 1.2). Stewart and Rohlich (1967) in their review of the different terms and definitions (blooms, Wasserblüte, Fleu de'eau, Flos aquae) concluded there was a real need to sharpen the terminology so that comparison of investigations would be possible, especially since discolouration of the water could be caused by other inert material. The most frequently used definition is that of Lackey (1945) - 500 cells per ml - but Lee (1970) would increase this range to 500 to 1000 cells per ml. These quantifications should take the place of earlier descriptions of the phenomenon, which involved the seasonal or pulse appearance of high algal growths (Stewart and Rohlich, 1967).

The meaning of the term water-bloom is of importance in discussion of Lake Ellesmere. The minimum mean cell concentration for the lake was 91,400 cells per ml in September 1978 (see Figure 6.4A), with a minimum for any single site at over 4,000 cells per ml. On a quantitative basis, therefore, Lake Ellesmere was in continuous bloom throughout the study period, and the general colour and turbidity of the water confirms this observation. Yet the qualitative use of the term has a seasonal implication plainly inappropriate to Lake Ellesmere. On only one occasion, subsequent to the continuous monitoring programme in March 1981, was a bloom of Nodularia spumigena observed to aggregate at the surface of the lake (see Appendix 2). This appearance was preceded by unusually warm, still weather conditions over a period of days.

The term water-bloom, and its equivalents should therefore be used in a more exact manner. As Stewart and Rohlich (1967) have urged, there is a need for quantification and this can also be carefully associated with the visual appearance of discolouration of the water. Quantification in terms of cell numbers is unsatisfactory because of the varying sizes of cells. Consequently it has been argued throughout this

study that cell biovolume is a more appropriate method to quantify phytoplankton standing crop (see section 6.3). Because Lake Ellesmere has been shown to be in continuous bloom condition, it is not possible to define a water-bloom in biovolume terms from this study.

Nevertheless, biovolume is a useful index of trophic status, because it is associated with the use of plant nutrients at the primary producer level. The biovolume index indicates the standing crop of the phytoplankton, avoiding problems of variation in cell size or variable pigment concentration between species. In assessing biovolume by direct observation, the aim must be to visually distinguish the cells from non-cellular detritis. The disadvantage of this method is the time required to count a sample.

In Lake Ellesmere, the maximum level of the biovolume index occurred at a different time from the peak in cell numbers. The maximum mean collection biovolume was 31.08 $cm^3.m^{-3}$ in February 1980 (section 6.3), whereas the maximum cell number was in May 1980. This again emphasizes the potential descrepancy between the two indices of standing crop. The minimum mean biovolume was 5.29 $cm^3.m^{-3}$ in August 1979.

Vollenweider (1971) gives guidance on estimating the trophic state of a water body according to biovolume densities. Surveying the literature he deduced that highly eutrophic lakes had biovolumes of greater than 10 $cm^3.m^{-3}$, and the transition being mesotrophic and eutrophic fell at about 3-5 $cm^3.m^{-3}$. On this index Lake Ellesmere again shows up as highly eutrophic. Even the minimum value in winter 1979 is within the eutrophic range.

Burns and Mitchell (1974) expressed the phytoplankton densities from Lakes Hayes and Johnson volumetrically. They found the maximum biovolume for Lake Johnson of 33.36 $cm^3.m^{-3}$ during a bloom of Anabaena flos-aquae and Peridinium cinctum, and for Lake Hayes of 7.49 $cm^3.m^{-3}$ with similar dominant organisms. They also found that the relative size of individual species often reflected the plankton count, so that on a percentage basis large dinoflagellates and cryptomonads were important components of the standing crop, even when not present in large numbers. The microalgae were very important numerically, but they comprised less than one per cent of the total volume of phytoplankton. Comparing these New Zealand lakes with

eutrophic lakes overseas, Burns and Mitchell compiled a ranked list of lakes based on the maximum phytoplankton volumes recorded. The range of volumes included was from 91.94 $cm^3.m^{-3}$ for Tystrup Sø, Denmark to 3.00 $cm^3.m^{-3}$ for Zurichsee, Switzerland. Lake Johnson was among the top three eutrophic lakes in their list. On the basis of the maximum level recorded in the present study, Lake Ellesmere would be among the top five eutrophic lakes, behind Tystrup Sø, Clear Lake (U.S.A.), Lake Johnson and Lough Neagh (Ireland).

The types of dominant algae within eutrophic lakes were listed in the compilation of eutrophic lakes by Burns and Mitchell (1974). It is striking that the dominant algae in all the other examples of eutrophic lakes were species of Cyanophyta (Aphanizomenon, Oscillatoria, Anabaena, Coelosphaerium), Bacillariophyceae (Melosira, Fragilaria, Asterionella, Tabellaria), Chrysophyceae (Dinobryon, Uroglena) or Dinophyceae (Peridinium). No cases of eutrophic chlorococcalean dominated lakes were included, yet in Lake Ellesmere Oocystis and Dictyosphaerium were the dominant genera at the time of the standing crop peak. Only one of the dominant organisms in Lake Ellesmere during 1978 - 1980 was not a green algae and that was the blue-green organism Microcystis minutissima.

The indirect indices of phytoplankton biovolume and cell numbers and the direct measures of nitrogen and phosphorus content of the lakewater furnish a similar conclusion about the trophic status of Lake Ellesmere. It is evident that the lake is in a highly eutrophic state, and Vollenweider's alternative term, polytrophic, seems very appropriate.

7.4 PHYTOPLANKTON

The phytoplankton flora of Lake Ellesmere has been described in detail (Chapter 5) and related to the physico-chemical environment (Chapter 6). Comparison has already been made in this discussion of the size of the standing crop in both numerical and biovolume terms (section 7.3).

This study of the phytoplankton of Lake Ellesmere has increased knowledge of the flora in the lake. About 12% of the flora recorded represented first sightings for New Zealand (section 5.5). This

highlights the general lack of knowledge of New Zealand phytoplankton, and the need for widespread surveys to be undertaken in a variety of habitats before a definitive work is compiled.

The composition of the flora was found to be largely chlorococcalean green algae, with important components of Cyanophyta and Chromophyta (section 5.5). The genera present within the flora were categorised on the basis of their habitats, whether freshwater, seawater or brackish-water and also with respect to a group with widespread tolerances. This compositional grouping shows some of the complexity in dealing with a brackish-water eutrophic system. One of the main approaches to organising lake genera is the 'community' approach. On this basis Hutchinson (1967) identified thirteen assemblages of genera representative of various trophic states. Cassie (1979) sought to apply the same categorisation to New Zealand lakes.

The dominant organisms in Lake Ellesmere were Dictyosphaerium spp., Oocystis spp., Planctonema lauterborni and Microcystis minutissima. The first two genera (four species included) are chlorococcalean; Planctonema is ulotrichalean, and Microcystis is a cyanophyte. Hutchinson (1967) suggested that a diatom community was most characteristic of eutrophic lakes, except at the warmest times, when chlorococcal dominants ordinarily occur in small lakes and ponds. The chlorococcal dominants are usually Pediastrum and Scenedesmus. Hutchinson viewed blue-green algal communities as essentially monospecific occurences in highly fertilized tropical waters. Although three species of Scenedesmus are recorded for Lake Ellesmere the population sizes were not at any time very large. So the community approach as propounded by Hutchinson does not seem valid for the present study.

Another discrepancy between the community-type concept and the evidence of the present study lies in the importance of Oocystis. Hutchinson (1967) sees Oocystis as a dominant organism primarily in oligotrophic lakes, although he recognised some discrepancies with the findings of Järnefelt (1952) for this genus. Yet three species Oocystis were important among the plankton of Lake Ellesmere. Oocystis parva had the greatest single mean biovolume at any one time over the sampling period (section 6.3.1).

The use of phytoplankton indices has not received much attention in this study. It was pointed out in an earlier section (5.5) that

Nygaard's (1949) indices could not be applied to Lake Ellesmere because of the complete absence of desmids. This is a direct consequence of the intolerance of desmids to brackish water, and again highlights the way that the location of the lake affects the phytoplankton population.

After an intensive survey of desmids in British lakes, Brook (1965) made a plea for the formulation of an index based on a limited number of species, the nutritional requirements of which had been investigated. The use of quotient indices in New Zealand studies has been slight. Bayly and Williams (1973) calculated indices for Lake Sarah, based on the data of Flint (1938); and Cassie applied quotient indices for Lake Rotorua (Cassie, 1969) and other North Island lakes (Cassie, 1978). The accuracy of such a method depends on the skill of identification. To these cautions about the use of quotient indices should be added the warning that such indices are not appropriate for brackish-water systems because of the complete absence of desmids.

The previous use of multivariate statistical analysis of phytoplankton data has not been widespread (see section 6.4). The two examples which used the same technique as this present study, reciprocal averaging, are by Happey-Wood (1980) and Baybutt and Makarewicz (1981). Happey-Wood studied the periodicity of Volvocales in shallow Priddy Pool, England. Species of Chlamydomonas and Chloromonas were sorted into seasonal patterns using reciprocal averaging. An eigenvalue of 0.218 for axes 1 and 2 was found. This compares favourably with the first two eigenvalues of 0.304 and 0.270 for the ordination of Lake Ellesmere data (see Table 6/14). The highest correlation of bicarbonate-alkalinity in Priddy Pool was with the first ordination axis and this suggested the importance of the overlying-water quality in regulating the flagellate community. Moss (1973a) also suggested that pH and the inorganic carbon equilibria in freshwater had an important role in determining the growth of algae. It is consequently not surprising that in Lake Ellesmere too pH, along with nitrate, is most highly correlated with the first ordination axis (section 6.4).

Baybutt and Makarewicz (1981) used several multivariate techniques, including reciprocal averaging, to analyse phytoplankton and water chemistry data from Lake Michigan for a 50 year period.

They illustrated the progression from oligotrophy to eutrophy, and a subsequent reversal of culturally accelerated eutrophication. Sodium and blue-green algal biomass were found to be significantly correlated, although phosphate enrichment, carbon dioxide availability and N:P ratios were also important.

A final comparison of results from reciprocal averaging studies is provided by Ogden and Caithness (1982). Although not relating to phytoplankton, it is a study undertaken within New Zealand on Pukepuke lagoon in the Manawatu, a shallow dune-lake. The open water area in this lagoon has been reduced markedly, due to a number of factors, including the spread of macrophytes. Ogden and Caithness describe the hydroseral development associated with the macrophyte swamp, and use a reciprocal averaging ordination to describe the extensive Typha stands. In their results 74% of the total variance was accounted for by the first two axes, although they did not indicate the number of axes extracted, or the associated eigenvalues. This result may be misleading if the residual variance is not included in the calculation. The first axis of the stand ordination correlated with water depth, pH and the depth of the underlying organic matter.

The final aspect to be discussed in relation to the phytoplankton of Lake Ellesmere is the question of limiting factors. It has been suggested (section 6.5) that the potential limiting factors controlling the plankton are nitrogen, phosphorus and carbon at various times of the year. Light was also thought to be limiting in terms of the euphotic depth due to high suspended solids content in the water column. Emphasis should again be placed on the use of the term 'potential limiting factor'. This study endeavours only to identify limitation based on field and chemical data, without supporting bioassays involving phytoplankton species.

There has been much debate during the last 25 years about the role of various factors in limiting growth of phytoplankton. This debate is highlighted in symposia such as Likens (ed., 1972), in which nitrogen and phosphorus were identified as key factors. The approach of the present study is based on empirical ratios between the cellular forms of carbon, nitrogen and phosphorus. Limitation was implied when the dissolved inorganic forms of these nutrients within the lakewater deviated from the expected cellular ratios.

(There is an underlying assumption that the cellular uptake reflects the lakewater ratios.) The implication of limitation when ratios varied from the expected was supported by the evidence of depletion of nutrients within the lakewater. This approach to nutrient limitation has received some support in the literature, including Chiaudani and Vighi (1974) and Niemi (1979).

Niemi (1979) discussed the occurrence and consequences of the N:P ratio in the Baltic Sea. He found that at times when the ratio was low, blooms of nitrogen-fixing blue-green algae occurred, particularly Aphanizomenon flos-aquae and Nodularia spumigena. In a bay where the N:P ratio was high, no algal blooms occurred. This phenomenon was probably due to the ability of blue-green algae to store surplus phosphorus in their cells, and transport it to the surface when they rise during warm still conditions. The algae which form the surface bloom showed a high rate of nitrogen fixation.

In Lake Ellesmere a period of supposed nitrogen limitation relates very well with the rapid population changes in blue-green algae. During the summer of 1979 - 1980 the N:P ratio dropped rapidly throughout the whole lake to a mean level of 0.63 (Fig. 6/22B). This was during a period of very high phytoplankton standing crop dominated by Oocystis spp. and Dictyosphaerium spp. From the time of nitrogen depletion (Collection 21; January 1980), the blue-green alga Microcystis minutissima increased rapidly until it was an important member of the phytoplankton community. Although this alga does not have heterocysts, it is evidently still able to thrive in the low nitrogen conditions.

The only noted surface bloom formation of Nodularia in Lake Ellesmere was in March 1981 (see Appendix 2). This was subsequent to the regular sampling programme and N:P ratios were not calculated. It was noted earlier, however, that surface bloom formation is very much associated with calm conditions whereas the period 1978-1980 was particularly windy (Section 3.3.3).

Nutrient limitation in New Zealand lakes has been demonstrated on a number of occasions. In nearly all cases nitrogen has been the limiting factor: Rotorua (Fish, 1971); Taupo (White and Downes, 1977); Johnson and Hayes (Mitchell and Burns, 1981). White (1982) has commented that low nitrogen levels and consequent low N:P ratios may

be an important characteristic of New Zealand freshwaters. Although this is partially supported by the present study, there is some conflicting evidence concerning the extent of nitrogen limitation in New Zealand. As already discussed (section 7.3), Lake Ellesmere has particularly high nitrate inflows from the surrounding agricultural catchment, unlike most other New Zealand lakes. Yet the evidence suggests that the lake can become nitrogen-limited during summer periods. Such summer limitation is very important, because this is the optimum growing period for phytoplankton. It has also been mentioned that the temperature range of the lake is unlikely to limit growth significantly during winter, at which time phosphorus was potentially limiting. During the spring period when growth characteristically speeds up, inorganic carbon was potentially limiting in localized areas, particularly near the inflows.

Light limitation must also be considered. The high turbidity reduces the euphotic zone to a very shallow level due to the biological population and the suspended sediments. Although this limits the light's penetration of the water, the wind does effectively assist the mixing of the phytoplankton. Individual cells are therefore likely to be within the euphotic zone for at least a short period of time.

Phytoplankton limitation due to light is not well documented in the literature. Javornický (1966) found that despite high nutrient concentrations coccoid algae were limited in development in the bottom of Slapy Reservoir in Czechoslovakia. The reservoir was thermally stratified and non-flagellated plankton did not move into the relatively thin euphotic layer. Only actively migrating flagellates and blue-green algae with a smaller specific weight than the water were found in the euphotic zone. On this account Javornický claimed that algal growth was retarded by unfavourable light conditions. Ahlgren (1979) in a study of an eutrophic Swedish lake showed that phytoplankton species were limited by both light and temperature. Hickman (1973) in a study of phytoplankton productivity in eutrophic Abbot's Pond, England considered that light was the most important limiting factor.

Green (1975) has discussed water transparency and light penetration in New Zealand lakes. Although it is not specifically related to light limitation, he listed the Seechi depth of a number

of lakes and suggested reasons in the case of lakes where water transparency was particularly low. He thought that humic material was the factor in dune and Westland lakes; glacial silt in high glacial lakes; and silt runoff from land and algal blooms in shallow coastal lakes. He included the Kaikoura lakes and Tomahawk lagoon in this final category, and Lake Ellesmere could also be placed here.

In summary, Lake Ellesmere although extremely shallow is highly eutrophic in comparison to other large New Zealand lakes, which are oligotrophic. The intensive agricultural catchment of Ellesmere has an important role in the supply of nutrients, which maintain the high trophic status. The lake is thus given nutrient loadings of nitrogen and phosphorus comparable to the Lakes Rotorua and Horowhenua. Ellesmere has been compared to Lakes Johnson and Hayes with regard to total algal biovolume, an indirect measure of trophic state. Other factors of importance in Lake Ellesmere are the climatic influences of wind in mixing the lake, moderate temperature regimes, and rainfall input over the full area of the lake surface. Perhaps one of the most important features of the lake, having a significant effect on the phytoplankton composition, is the occasional influx of seawater. In this respect it is similar to Lake Forsyth with a comparable floral composition in both lakes. The limitation of phytoplankton in Ellesmere has been attributed to nitrogen in summer 1980, despite high concentrations of nitrate. Further limiting factors include phosphorus in winter, carbon for short periods in spring and light due to high turbidity for much of the year.

CHAPTER 8

CONCLUSION AND SUMMARY

1. Lake Ellesmere is a large shallow lake on the margin of the Canterbury Plains. This location has a particular influence on the nutrient regime and the ionic composition of the lakewater.

2. Because Lake Ellesmere is shallow, wind action results in turbid lakewater due to resuspension of non-biological sediment from the bottom of the lake. Wind action also maintains the phytoplankton within the water column.

3. Rainfall makes an important contribution to the hydrology of the lake.

4. Nutrient content of the lakewater is very high. When compared with data available for other New Zealand lakes, Lake Ellesmere has some of the highest levels for both nitrogen and phosphorus.

5. Trophic status is defined primarily in terms of plant nutrient content. On this basis, Lake Ellesmere is described as highly eutrophic (polytrophic).

6. Lake Ellesmere is in a continuous water-bloom condition throughout the year with green and blue-green algae. Nodularia spumigena sometimes forms surface scums during still water conditions.

7. Other indices of eutrophication used in this study are total cell numbers and total biovolume. Both of these measures confirm the trophic status and indicate Lake Ellesmere to have some of the highest phytoplankton standing crops for New Zealand lakes.

8. The phytoplankton flora of the lake is composed largely of chlorococcalean Chlorophyta, with important members of Cyanophyta and Chromophyta. The genera present in the lake originate from freshwater, marine and brackish water. Desmids are completely lacking in the lake.

9. The dominant phytoplankton are Dictyosphaerium spp., Oocystis spp., Planctonema lauterborni and Microcystis minutissima. These organisms form a series of dominant/sub-dominant communities.

10. Reciprocal averaging ordination of the phytoplankton sample data can be used to separate the samples and species into independent axes. The first three eigenvalues from the ordination account for about 38% of the variability within the data. Nitrate and pH are the most highly correlated variables on the first axis. This compares favourably with comparable studies on phytoplankton.

11. Nutrient limitation has been assessed based on lakewater supply ratios and depletion of supply within the lake. Phosphorus limitation in winter is followed by a brief period of carbon limitation in the vicinity of the inflows in spring, and then nitrogen limitation in summer. Wide areas of the lake are nutrient limited for much of the year.

12. A shift in the composition of the phytoplankton flora was observed at the time of widespread nitrogen limitation. This shift included an increase in blue-green algae.

13. Light penetration is restricted within Lake Ellesmere. This limits the euphotic zone, but the action of the wind in mixing the lake maintains the phytoplankton within the euphotic zone.

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APPENDIX 1

UNITS AND ABBREVIATIONS

SI units (Systeme International d'Unites) have not been used widely in limnological literature. Therefore conversion of published results are often required before comparison of data can be made. To enable a quick conversion the following equivalents are given:

Chemical concentration:

$g.m^{-3} = mg.l^{-1}$

$= ppm$ (parts per million)

Mass Flow:

$g.s^{-1} = 86.4\ kg.d^{-1}$

Conductivity:

$mS.m^{-1} = 10\ \mu S.cm^{-1}$ (= 10 $\mu mho.cm^{-1}$)

= (approx.) 10^{-3} meq. l^{-1}, depending on the nature of the dissolved salts (Golterman, 1975a).

Other abbreviations in this study have included:

B.P.	before present
D.S.I.R.	Department of Scientific and Industrial Research
N.C.C.B.	North Canterbury Catchment Board
O.E.C.D.	Organisation for Economic Co-operation and Development

APPENDIX 2

Occurrence of Nodularia spumigena in Lake Ellesmere

Nodularia spumigena appeared in Lake Ellesmere in 1971 and bloomed in the lake in 1972 (Hughes et al., 1974). During the present study it was only recorded on two occasions: in March 1978 and again in March 1981.

In March 1981 a severe bloom was reported from a widespread area of the lake (T. Dodgson, Fisheries Research Division, Ministry of Agriculture and Fisheries, pers. comm.). This bloom was the worst that fishermen in the area had ever seen and occurred in the following areas: off the Halswell River, along the Kaitorete Spit, near Taumutu, in a large area off Lakeside and in the embayment to the west of the Selwyn delta. At the time the conditions were "as calm as a mill pond" and warm. After four days, surface scum was evident along the margins of the lake, while out on the lake it was largely broken up by the action of the wind. A light easterly wind was forming a slight ripple on the lake surface, but on the leeside of the stationary boat, the Nodularia rose again quickly.

Nodularia spumigena has been reported from Lakes Rotorua and Rotoiti (Cassie, 1974); Lake Taharoa and Waitakere Stream (Sarma and Chapman, 1975); Lakes Forsyth and Ellesmere (Flint, 1975). The overseas distribution includes Australia (Williams, 1969), South Africa (Hutchinson et al., 1932), Canada (Nordin and Stein, 1980) and Europe (Ostrom, 1976).

Nordin and Stein (1980) studied the ecology of the species and found salinity was the most important factor in its distribution. Optimum growth occurred when salinity was 5-20‰ NaCl. Marine waters contain NaCl but inland water bodies containing Nodularia were composed mainly of Na_2SO_4, $MgSO_4$ and Na_2CO_3.

Nodularia spumigena is thought to be toxic and responsible for killing steers, dogs and sheep (Conner, 1977; Cassie, 1979).